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**University of Alberta**

**Mortality models for major boreal mixedwood species in Alberta**

by

Yuqing Yang ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of  
the requirements for the degree of Doctor of Philosophy.

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Spring 2002





**University of Alberta**

**Faculty of Graduate Studies and Research**

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Mortality models for major boreal mixedwood species in Alberta**, submitted by **Yuqing Yang** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in *Forest Biology and Management*.





## Abstract

This thesis focused on mortality model development for three major boreal mixedwood species in Alberta: trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm).

An individual tree survival function was developed for each species using a generalized logistic function. Measurement interval length entered the logistic equations as an exponent to overcome the problem of unequal measurement intervals. Unknown parameters were estimated using the maximum likelihood method. The newly developed functions were compared to the old ones previously used by the Mixedwood Growth Model (MGM). Both fitting and validation results confirmed that the new functions performed better than the old ones. MGM simulations further supported this conclusion.

The self-thinning concept was used to develop a maximum size-density relationship between quadratic mean diameter and stand density. Several functions were compared first by fitting an average size-density relationship and two equally good functions were selected based on model fitting and prediction statistics. They were then refitted with a specially defined loss function to derive the maximum size-density relationship. One final function was chosen as a stand level constraint on the empirical survival functions in MGM. It was found that site quality did not affect this maximum size-density relationship and separation of this relationship by species was not possible.



Besides the maximum size-density relationship, a group of constraining factors were also developed to further constrain the empirical survival functions. One factor was based on the idea that there is a maximum basal area a stand can produce and this maximum basal area is different for different species. This factor was developed to prevent excessive yields for very dense stands. Another factor was developed to reduce the survival rates of very old trees based on a defined quadratic mean diameter limit for each species. The third factor was based on the average height growth rate of the top height trees in a stand and was developed to break up short-lived aspen and lodgepole pine stands at old ages. Imposing these factors on the empirical survival functions assures ecologically reasonable performance of MGM when extrapolated beyond the typical data range used for model development.





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# Chapter 1. Introduction

Growth and yield information is fundamental to forest management. It has been widely used for long-term strategic planning, updating and projecting forest inventory, providing input for timber supply planning and harvest scheduling, and evaluating stand performance and cultural alternatives (Harrison and Daniels 1988). Well-developed growth and yield models can provide accurate and timely information and have been used widely by resource managers for management planning and decision-making.

A major component of a growth model is mortality, which is less well modeled in general due to the complexity involved in the mortality process (Buford and Hafley 1985). This is particularly so in multi-species boreal mixedwood stands. However, it is crucial to have a reliable mortality component since it ultimately determines the accuracy of growth and yield predictions. This thesis focuses on mortality modeling for major tree species of the boreal mixedwood forest in Alberta. The purpose of this chapter is to provide background information on the subject generally and then on the need for mortality models. It outlines the goals for the thesis research and then outlines the remaining chapters.

Boreal forests are important ecosystems. They account for 8% of all forested lands and 26% of closed-canopy forests around the world (Rowe 1993). Out of Canada's 8 forest regions (Rowe 1972), the boreal forest region is the largest one that forms a continuous belt from Newfoundland to Yukon. It occupies about 35% of the total land area and 80% of the total forested area of Canada (McLaren 1990, Rowe 1993, Anonymous 1998). Among the 6 natural regions in Alberta, the boreal forest region is the largest one, comprising more than half (52.3%) of the total land area. Therefore, it is very important to model the growth and yield of boreal forests accurately for better management practices. Since a significant portion (about 85%) of Alberta's boreal forests is composed of mixedwood stands (Achuff 1994, Anonymous 1998), it is even more important to model the growth and yield of boreal mixedwood forests.



As discussed by Vanclay (1994), a lot of growth models have been developed for pure-species even-aged stands, especially for plantations. However, these ecosystems are rather simple. here has only been limited effort to quantify growth and yield relationships for mixedwood stands (Burkhart and Tham 1992). Due to the variety of possible species mixtures, modeling of mixed-species forests has been less successful. Therefore, it is more challenging and more urgent to develop reliable growth models for complicated ecosystems such as boreal mixedwood forests.

It is very important to model mortality. Firstly, mortality is a key process in stand dynamics. The death of a single canopy tree or a group of canopy trees will release the available growing space and create a gap. In time, this gap will be occupied again by lateral growth of surrounding trees, by releasing advance regeneration, or by new recruitment (Oliver and Larsen 1996). Gap size is a major factor in determining forest regeneration dynamics. Depending on the size of a gap, shade-tolerant and shade-intolerant species regenerate differently (Shugart 1984, Brokaw 1985, Platt and Strong 1989, Raich and Gong 1990). Gap dynamics determines forest species composition, stand structure and process (McCarthy 2001). Reliable prediction of the mortality rate of each individual tree is therefore a prerequisite for accurate prediction of stand dynamics.

Secondly, tree mortality is a very complicated process and is influenced by a variety of factors, such as environmental, physiological, pathological, entomological factors, and some random events. It is very difficult to describe tree mortality accurately only by a mathematical model. Although many mortality models have been developed for various tree species and stand types around the world, successes are rare and mortality remains one of the least understood components of growth and yield estimation (Hamilton 1986, Monserud and Sterba 1999). The mortality component is also the major source of variability in yield predictions and the contribution to the total variability increases as projection period increases (Stage and Renner 1988, Gertner 1989). The needs for better mortality models are apparent.

Several approaches are available for mortality modeling. Among them are artificial neural networks (Guan and Gertner 1991a, 1991b, 1995), non-parametric classifiers (Dobbertin and Biging 1998), cross-classification (Buchman et al. 1983), and regression (Monserud 1976, Hamilton and Edwards 1976, Monserud and Sterba 1999).



Artificial neural networks, also known as parallel distributed processing systems, are composed of several feed-forwarding layers. There are two major components: processing units and a group of weights connecting the processing units in a network. Processing units are responsible for receiving signals and sending those signals out to other units. An error function of the network is minimized to achieve the desired results through weight adjustments. An appropriate training algorithm has to be developed first and this is still a problem with the approach. Another major disadvantage with this method is that convergence is very slow (Guan and Gertner 1995). More research is needed before this method can be widely applied in mortality modeling. In addition, no significant improvement is achieved using this method compared to traditional regression methods (Monserud and Sterba 1999).

Non-parametric classifiers employ a recursive-partitioning technique. A binary classification tree (CART) is used to split the data set into two increasingly homogeneous subsets (dead and alive). The rule of Bayes is used for data split. However, Dobbertin and Biging (1998) revealed that the prediction accuracy is about the same as logistic models for the two species studied. They also emphasized that inferences from their work are limited and more repetition is necessary to verify this methodology.

Using the cross-classification, data with similar characteristics (e.g., similar size classes or age classes) are assigned to the same cell and the survival rate of each cell is simply the ratio of live trees to total number of trees in that cell. Although simple to apply, this approach requires a large data set to ensure that there are no empty cells or cells with only a few trees (Guan and Gertner 1995).

The regression approach is by far the most widely used approach for mortality modeling. Permanent sample plot data are typically used for this purpose. Stand or individual tree characteristics are employed directly to fit a mathematical model to predict stand level or individual tree level mortality. It is a statistical method where unknown parameters are estimated in such a way that the deviations between the fitted function and the actual data are minimized. Stand level mortality models predict stand density changes over time, while individual tree mortality models predict the probability of survival or mortality for each individual tree involved in growth projections (Clutter et al. 1983). To make better





management decisions, we need not only the number of dead trees, but also the species and sizes of those trees. Individual tree mortality models, though more complicated, can provide the required information and are often preferred from a management perspective, especially for intensive forest management.

There are two types of mortality, regular and irregular. Regular mortality refers to mortality caused by competition, or mortality due to old age and small scale attacks from insects, diseases, and some random events. Irregular mortality relates to incidents such as fire, windthrow, and outbreak of insect infestation and diseases. It is generally associated with large-scale tree death within a short period of time (Lee 1971, Monserud 1976, Dobbartin and Biging 1998). Like most studies on mortality modeling, this study only deals with regular mortality.

This thesis work is under the framework of the Mixedwood Growth Model (MGM) developed at University of Alberta. "MGM is a deterministic, distance-independent, individual tree based stand growth model that is capable of summarizing both tree and stand characteristics for major boreal mixedwood species" (<http://www.rr.ualberta.ca/research/mgm/mgm.htm>). MGM simulations showed that growth projections were very sensitive to the mortality component. Major variability in projected stand yields was caused by the mortality functions. In addition, unrealistic stand yields were detected when MGM was extrapolated outside the typical data range. Again, the mortality functions seemed to be the major cause. The need for re-developing or adjusting these mortality functions is urgent.

The overall objective of this thesis was to identify the limitations of the mortality model used in MGM (Yao et al. 2001) and to re-develop it. The following objectives were set:

- 1) To identify ecologically or biologically important predictor variables for mortality modeling
- 2) To refit the empirical mortality functions for three major boreal mixedwood species
- 3) To develop a maximum size-density relationship based on the self-thinning concept
- 4) To develop several constraining factors on the empirical mortality functions to ensure reasonable model behavior when extrapolated beyond typical stand conditions where data is available.



Working towards these objectives, Chapter 2 presents the ecologically important predictor variables and the development of a new empirical mortality function for each species studied. These new functions were compared with the old ones (previously used in MGM) using both model fitting and model validation statistics. In addition, they were also carefully examined for possible ecological deficiencies through MGM simulations. Although the newly developed mortality functions behaved better than the old ones, they still gave unsatisfactory results when extrapolated. This is a general problem with empirical models, which is caused by the lack of data in certain stand conditions. Until more broad range data become available, other methods have to be employed to ensure reasonable model predictions.

Based on the self-thinning concept, Chapter 3 describes the development of a maximum size-density relationship between quadratic mean diameter and stand total density. This relationship was not affected by site quality and it was not separable by species. It was used to constrain the empirical mortality functions developed in Chapter 2. For any stand, if the combination of quadratic mean diameter and total density is above the maximum size-density curve, smaller trees receive more reduction on their survival rates compared to larger ones to bring the stand back on or below the maximum curve.

The maximum size-density relationship alone does not always ensure reasonable model projections. Several other constraining factors based on biological and ecological theories were developed and they are described in Chapter 4 and served as theoretical constraints on the empirical mortality functions. These factors, together with the maximum size-density curve, ensure reasonable stand projections across a wide range of stand and site conditions.

The results of this study are summarized in the last chapter, Chapter 5. The significant contributions of this work are also discussed in this chapter. In addition, future research needs are identified.

## References

Achuff, P.L., 1994. Natural regions, subregions and natural history themes of Alberta. A classification for protected areas management. Protected areas report No. 2, prepared for Parks Services, Alberta Environmental Protection, Edmonton, AB, 72 p.





- Anonymous, 1998. The boreal forest natural regions of Alberta. Alberta Environmental Protection, Natural Resources Service, Recreation and Protected Areas Division, Natural Heritage Planning and Evaluation Branch, 313 p.
- Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. *Ecology*, 66, 682-687.
- Buchman, R.G., Pederson, S.P., and Walters, N.R., 1983. A tree survival model with application to species of the Great Lakes region. *Can. J. For. Res.*, 13, 601-608.
- Buford, M.A., and Hafley, W.L., 1985. Probability distributions as models for mortality. *For. Sci.*, 31 (2), 331-341.
- Burkhart, H.E., and Tham, A., 1992. Predictions from growth and yield models of the performance of mixed-species stands. In: M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson (eds). *The ecology of mixed-species stands of trees*. Blackwell scientific publications, Oxford, 312 p.
- Clutter, J.L., Fortson, J.C., Pienaar, L.V., Brister, G.H., and Bailey, R.L., 1983. *Timber management: a quantitative approach*. Wiley, New York, 333 p.
- Dobbertin, M., and Biging, G.S., 1998. Using the non-parametric classifier CART to model forest tree mortality. *For. Sci.*, 44 (4), 507-516.
- Gertner, G.Z., 1989. The need to improve models for individual tree mortality. *In*: Seventh central hardwood forest conference. pp. 59-61. USDA For. Serv. Gen. Tech. Rep. NC-132.
- Guan, B.T., Gertner, G.Z., 1991a. Using a parallel distributed processing system to model individual tree mortality. *For. Sci.*, 37 (3), 871-885.
- Guan, B.T., Gertner, G.Z., 1991b. Modeling red pine tree survival with an artificial neural network. *For. Sci.*, 37 (5), 1429-1440.
- Guan, B.T., Gertner, G.Z., 1995. Modeling individual tree survival probability with a random optimization procedure: an artificial neural network approach. *AI Applications*, 9 (2), 39-52.
- Hamilton, D.A. Jr., 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. *For. Sci.*, 32, 989-1000.
- Hamilton, D.A. Jr., and Edwards, B.M., 1976. Modeling the probability of individual tree mortality. USDA For. Serv. Res. Pap. INT-185, 22 p.
- Harrison, W.C., and Daniels, R.F., 1988. A new biomathematical model for growth and yield of loblolly pine plantations. *In*: A.R. Ek, S.R. Shifley, and T.E. Burk (eds). *Forest growth and yield modeling and prediction*. pp. 293-304. USDA For. Serv. Gen. Tech. Rep. NC-120, Vol. 1.



- Lee, Y.J., 1971. Predicting mortality for even-aged stands of lodgepole pine. *For. Chron.*, 47, 29-32.
- McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.*, 9, 1-59.
- McLaren, C., 1990. Heartwood. *Equinox*, 53, 42-55.
- Monserud, R.A. 1976. Simulation of forest tree mortality. *For. Sci.*, 22, 438-444.
- Monserud, R.A., and Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.*, 113, 109-123.
- Oliver, C.D., and Larson, B.C., 1996. Forest stand dynamics. Update edn, John Wiley & Sons, Inc., 520 p.
- Platt, W.J., and Strong, D.R., 1989. Special feature - treefall gaps and forest dynamics. *Ecology*, 70, 534-576.
- Raich, J.W., and Gong, W.K., 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. Ecol.*, 6, 203-217.
- Rowe, J.S., 1972. Forest regions of Canada. Revised. Can. Dep. Fish. & Environ., Can. For. Serv., Ottawa, ON. Publ. 1300, 172 p.
- Rowe, J.S., 1993. Boreal forest in the global context. *In*: The National and Global Crisis in Canada's Forests. pp. 5. Canada's Future Forest Alliance, New Denver, BC.
- Shugart, H.H., 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York, 278 p.
- Stage, A.R., and Renner, D.L., 1988. Comparison of yield-forecasting techniques using long-term stand histories. *In*: A.R. Ek, S.R. Shifley, and T.E. Burk (eds). Forest growth and yield modeling and prediction. pp. 810-817. USDA For. Serv., Gen. Tech. Rep. NC-120, Vol. 2.
- Vanclay, J.K., 1994. Modeling forest growth and yield: applications to mixed tropical forests. CAB International. Wallingford, UK, 312 p.



## **Chapter 2. Development of individual tree mortality functions for major boreal mixedwood species**

### **2.1. Introduction**

Mortality of trees is a very complicated process and is affected by a variety of factors, such as environmental, physiological, pathological, and entomological factors, as well as some random events. Tree death is generally the result of complex interactions among multiple factors and is often a gradual process, although it can be abrupt sometimes (Franklin et al. 1987, Waring 1987). Some factors will weaken trees while others directly cause tree death (Manion 1981). In general, trees die when they can't acquire or mobilize sufficient resources to maintain growth or to heal injuries (Waring 1987). However, there might also be quick death for healthy trees when exposed to sudden stress like draughts, frosts, or insects.

Due to the complexity of the mortality process and the uncertainty in the timing of tree death, mortality remains one of the least understood components of growth and yield estimation (Lee 1971, Hamilton 1986, Dobbartin and Biging 1998). For example, Stage and Renner (1988) found that most (80%) of the variability in volume predictions for mixed conifer forests in the Rocky Mountains region (US) was due to the uncertainty in mortality estimates.

Although complicated, some generalities on tree mortality can be derived. Hamilton (1986) stated that variation in tree mortality could frequently be explained by a measure of tree size, stand density, individual competition, and tree growth rate. During the last few decades, many mortality models have been developed for different stand types and tree species.

Linear and polynomial functions of stand and individual tree level variables were commonly used to model mortality in the 60's and 70's (Coile and Schumacher 1964, Bella 1970, Lee 1971, Lenhart 1972, Smalley and Bailey 1974, Feduccia et al. 1979). These mortality models may perform well within the data range upon which they were developed. However, the functional forms are often not compatible with the ecological and biological behavior of tree growth and mortality. Therefore, the predicted probability of mortality is not guaranteed to be in the range [0,1], which is a critical requirement for mortality modeling (Hamilton 1974).





Many nonlinear functions are implicitly defined between zero and one. Among them, a group of cumulative probability distributions have been used for mortality modeling. Examples include the negative binomial distribution (Cunia 1974, Hafley et al. 1982, Buford and Hafley 1985), the Weibull distribution (Somers et al. 1980, Buford and Hafley 1985), the gamma distribution (Buford and Hafley 1985, Kobe and Coates 1997), and the exponential distribution (Moser 1972).

Starting with Walker and Duncan (1967) and Neter and Maynes (1970), the logistic function has been the most widely used function for mortality modeling. It has been adopted to model the probability of survival or death of individual trees for various tree species (Hamilton 1974, 1990, Hamilton and Edwards 1976, Monserud 1976, Hann 1980, Wykoff et al. 1982, Buchman et al. 1983, Lowell and Mitchell 1987, Vanclay 1991, Avila and Burkhart 1992, Monserud and Sterba 1999, Cao 2000). Efforts have been devoted to selecting better predictors, estimating parameters accurately, and developing variants of logistic models (Guan and Gertner 1991).

Logistic regression was also adopted by Yao et al. (2001) to model the probability of survival for three major tree species in Alberta: trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm). The mortality functions developed for the three species are:

$$P_1 = \left( 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * SC_{SW} + \beta_5 * SPI/BA + \beta_6 * DBH^2/BA)) \right)^{-L} \quad (1)$$

$$P_2 = \left( 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * SPI + \beta_5 * DBH^2/BA)) \right)^{-L} \quad (2)$$

$$P_3 = \left( 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * BA + \beta_5 * SC_{PL} + \beta_6 * SPI + \beta_7 * DBH^2/BA)) \right)^{-L} \quad (3)$$

where

$P_1$  = annual survival probability of an aspen tree

$P_2$  = annual survival probability of a white spruce tree

$P_3$  = annual survival probability of a lodgepole pine tree

DBH = individual tree diameter outside bark at breast height (1.3 m above ground) (cm)



DIN = annual diameter increment (cm)  
 BA = stand total basal area (m<sup>2</sup>/ha)  
 SPI = site productivity index, defined as the average height of the dominant and codominant trees at 20 cm reference-diameter (m)  
 SC<sub>sw</sub> = white spruce species composition, defined as the ratio of white spruce basal area to stand total basal area  
 SC<sub>pl</sub> = lodgepole pine species composition, defined as the ratio of lodgepole pine basal area to stand total basal area  
 L = measurement interval length (yrs)  
 $\beta_0 \sim \beta_7$  = estimated coefficients.

Equations (1), (2), and (3) will be referred to as old survival functions from now on and the functions to be developed in this study will be referred to as new survival functions. Closer examination of the old survival functions revealed several problems.

One major problem with the old survival functions is that species interactions are not well modeled in typical mixedwood stands of aspen and white spruce. This is a twofold problem. Firstly, understory white spruce trees have a big negative impact on the annual survival rates of overstory aspen trees and this impact increases dramatically with increasing spruce density. This is contradictory to the well-accepted ecological expectation. In typical boreal mixedwood stands of trembling aspen and white spruce, aspen usually dominates the canopy layer for an extended period of stand development with white spruce trees remaining in the understory. Understory white spruce trees should have very little, if any, negative impact on the growth and survival of overstory aspen trees (Kabzems et al. 1986, Kelty 1989). Larger aspen trees are expected to be more competitive over smaller spruce trees.

Secondly, by using the old survival functions, the annual survival rates of understory white spruce trees are reduced a lot when there are aspen trees present in the overstory. This does not agree with the associated ecological theory. When overstory aspen density is low, there is enough light reaching the understory and there should be little spruce mortality. In fact, the survival rates of newly regenerated white spruce trees might even be improved by shading from a small amount of aspen in the overstory. Lieffers and Stadt (1994) demonstrated that the



amount of competing vegetation in the understory could be effectively reduced with a small amount of overstory aspen trees. Overstory aspen trees can also protect the understory white spruce seedlings from severe weather conditions such as heat or frost. Therefore, lower density aspen canopy should have very little negative impact on the survival of understory spruce. The negative impact increases with increasing overstory aspen density.

Another problem is associated with volume predictions. MGM projections showed that for all three species, the volume predictions are too low for stands with very low densities. This might be so in declining stands but it is not the case for healthy low-density stands. Prediction results revealed that the survival functions previously used in MGM were responsible for this. The objectives of this study were to evaluate various potential predictor variables and to refit the survival functions for aspen, white spruce, and lodgepole pine to achieve better predictions. Only regular mortality caused by competition, old age, and small-scale attacks from insects, diseases were modeled. A model with good ecological behaviors is preferred over a model with purely good statistical fits. Therefore, efforts were devoted to selecting those variables that are ecologically important to tree mortality. Potential functions should be evaluated against ecological theories to ensure reasonable model performance over a wide range of stand conditions.

## **2.2. The data**

This study used Permanent Sample Plot (PSP) data collected by Alberta Land and Forest Service over the past 4 decades. The data were from 699 locations and covered wide ranges of stand ages, stand densities, species compositions, and site conditions in the province of Alberta. At each of the 352 locations there was a cluster of 4 plots, while there was only one plot at each of the remaining 347 locations. Detailed information can be found in the permanent sample plot field procedure manual (Alberta Land and Forest Service 1998).

Altogether, there were 1755 plots with up to six re-measurements. Table 2.1 summarizes the major variables used in this study. For each species, the number of trees, the mean, the standard deviation, the maximum, and the minimum are given by tree status (survivor trees and mortality trees) for the following variables: diameter, diameter increment, measurement interval length, stand basal area, basal area of larger trees, basal area of taller trees, and





species composition by basal area. Species composition is defined as the ratio of a species basal area to stand total basal area. All three types of basal areas are broken down into coniferous and broadleaf groups and summarized in Table 2.1. Data with obvious measurement errors are deleted. For example, trees with diameter increments larger than 1 cm or smaller than -0.5 cm are deleted. Based on the growing conditions in Alberta and the sizes of trees with large diameter increments (diameters > 15 cm), 1cm is used as the upper diameter growth limit. For each species, only a few trees in the fitting data set have diameter increments smaller than -0.5 cm and this value is subsequently used as the lower limit. For all three species, only less than 0.14% of trees are deleted.

Re-measured permanent sample plot data are correlated temporally. This violates the basic assumption of independent error terms in most statistical methods. When error terms are correlated, the estimated coefficients are still unbiased and consistent, but the variances associated with these coefficients are no longer the minimum variances. The calculated mean squared error may underestimate the real variance of the error terms and the calculated standard deviations of the estimated coefficients may underestimate the real standard deviations. Consequently, the t test, the F test, and confidence intervals are not valid any more (Kozak 1997). Since the estimated coefficients are still unbiased and consistent, this correlation problem is generally ignored for prediction purposes (Buchman et al. 1983). Gertner (1987) reported that as measurement interval length increased, auto-correlation decreased in roughly an exponential fashion. Borders et al. (1987) found that for permanent sample plot data with more than 3 re-measurements, auto-correlation did not occur for non-overlapping growth intervals. However, obvious auto-correlation occurred when all possible growth intervals were used. Huang (1997) concluded that for prediction purposes, whether the correlation was accounted for or not had little practical significance.

Measurement intervals are generally quite long in Alberta PSP data (see Table 2.1). In addition, the developed model will be mainly used for predictions. Therefore, auto-correlation problem was ignored in this study. However, to be cautious, only data from non-overlapping measurement intervals were used. Specifically, only data from the first three measurements were used. Diameter increment was calculated using data from the first two measurements and data from the third measurement were used to determine the mortality status of each individual tree (alive or dead). With the diameter increment and the mortality status



information ready, data from the second measurement were used to develop the new survival functions. For white spruce and lodgepole pine, only data from plot 1 were used for model fitting due to the large number of plots and trees measured. Data from plot 2 were used for model validation. Since there were fewer plots and trees measured for aspen, 65% of all the data were randomly selected and used for model fitting. The remaining 35% of the data were used for model validation.

Mortality is a discrete event. At each measurement, a tree was either alive or dead. Therefore, the dependent variable (mortality status) was a dichotomous variable. In this study, the dependent variable was coded as 1 for trees alive at both ends of the measurement interval, and as 0 for trees that were alive at the beginning of the measurement interval but were dead at the end of the measurement interval. The predicted probability of survival will be in the range  $[0,1]$  with 0 being dead and 1 being alive.

## **2.3. Model development**

### **2.3.1. Variable selection**

As pointed out by Hosmer and Lemeshow (1989), successful modeling of a complex data set is partly science, partly statistical methods, and partly experience and common sense. The more variables included, the more dependent on the data the model becomes. Assessing tree mortality is a diagnostic problem and a variety of variables should be evaluated. A tree's probability of survival depends on its genetic makeup and its environment (Saveland and Neuenschwander 1990). As much as possible, the selected predictor variables should reflect these factors.

The physiological processes involved in individual tree growth and stand development are complex. Although biological and ecological investigations are continually advancing our qualitative understanding of these processes, our quantitative understanding is far less developed. Many growth and yield models are statistical models and have only limited, if any, biological interpretation (Tait and Jahraus 1988). Understanding of the biological processes associated with tree growth can help modelers in two ways. Firstly, it helps modelers to formulate hypotheses, select potential predictor variables, and determine the relationships for model development. Secondly, it is helpful for proper evaluation and interpretation of



alternative model forms. Any relationship that violates accepted biological principles should be rejected, even if it results in efficient predictions for a particular data set (Hamilton 1990).

Numerous studies revealed many variables that were important for mortality predictions and they were examined here as potential variables.

### **Diameter at breast height**

In uneven-aged forests like boreal mixedwood forests, information on individual tree age is usually lacking. Tree size (usually diameter) has been used as a proxy of tree age by many people (e.g., Yao et al. 2001). However, as shown by several studies (Harper 1977, Silvertown 1982, Hughes 1984, Kirkpatrick 1984), tree size might be a better variable for mortality predictions than tree age since the birth or death of many organisms may depend more on the size than the age of an individual. Therefore, no attempt was made in this study to find the best variable to represent tree age. Instead, individual tree diameter was selected as a primary predictor variable. This variable has been widely used in individual tree mortality models (e.g., Monserud 1976, Buchman et al. 1983, Vanclay 1991, Avila and Burkhart 1992, Monserud and Sterba 1999, Yao et al. 2001).

### **Diameter and diameter squared**

Tree mortality rate generally decreases as tree size increases in all-aged forests (Silvertown 1982). However, Goff and West (1975) argued that as trees continue to grow larger, mortality rates start to pick up again. Larger trees are normally associated with old ages with very small growth rates. They become vulnerable to disease, wind, and other mortality agents. Therefore, a U-shaped mortality trend is probably expected (Buchman et al. 1983, Lorimer and Frelich 1984, Harcombe 1987, Monserud and Sterba 1999), i.e., mortality rates are high for juvenile trees, decrease with increasing tree sizes, and start to increase again with further increase in tree sizes.

To examine if the U-shaped mortality trend is present in the data set used in this study, annual mortality rates were calculated using all available PSP data, assuming constant mortality rate within each measurement interval. Assuming constant annual mortality rate is quite common for data measured several years apart (Hamilton and Edwards 1976, Lorimer 1981, Buchman





and Lentz 1984, Buchman 1985, McCune and Cottam 1985).

The calculated annual mortality rates were first grouped into 3 measurement interval classes: short intervals ( $<6$  yrs), medium intervals ( $\geq 6$  and  $\leq 11$  yrs), and long intervals ( $>11$  yrs). Within each measurement interval class, the mortality rates were further grouped into 3 site classes: good sites ( $>19$  m), medium sites ( $\geq 11$  m and  $\leq 19$  m), and poor sites ( $< 11$  m). For each site - interval combination, several 10 cm diameter classes (6 for aspen and lodgepole pine; 8 for white spruce) were created to detect the mortality trends. Fig. 2.1 shows the averaged annual mortality rate for each class generated. Each diameter class is labeled by its midpoint value. The U-shaped mortality trend is apparent for almost all the site-interval combinations with the exception of lodgepole pine with short intervals. Lack of larger dead trees in the short intervals of lodgepole pine might be the reason.

Given the general U-shaped mortality trend in the data, individual tree diameter and diameter squared were both selected as predictor variables to capture this trend.

### **Diameter increment**

Buchman et al. (1983) indicated that diameter increment of a tree strongly influenced its mortality rate. Dobbertin and Biging (1998) reported that mortality rates were higher for trees with reduced growth rates. A thinning study (Johnstone 1997) showed that tree vigor was improved greatly with larger diameter increments and the risk of insect and disease induced loss was reduced accordingly. This variable has been frequently used for modeling individual tree mortality (Monserud 1976, Buchman et al. 1983, Hamilton 1986, Hamilton 1990).

Fig. 2.2 presents the mean diameter increments by diameter classes and tree status (survivor trees and mortality trees). It is clearly shown that for all three species, the overall mean diameter increment of live trees is much larger than that of the dead trees. The same conclusion holds when diameter increments are grouped by diameter classes. These results demonstrate that diameter increment is indeed an important variable in describing tree mortality. Yao (1997) also confirmed this by reporting survival functions with and without diameter increment as a predictor variable.



When calculating diameter increment using the PSP data not measured annually, it is assumed that annual diameter growth is constant between two consecutive measurements. To verify this assumption, those plots with at least three measurements were used. Annual diameter increment (DIN) of a tree was calculated using its diameter at the first measurement (DBH<sub>1</sub>) and its diameter at the third measurement (DBH<sub>3</sub>):

$$DIN = (DBH_3 - DBH_1) / (L_1 + L_2)$$

where

$L_1$  = measurement interval length (years) between the 1<sup>st</sup> and the 2<sup>nd</sup> measurements

$L_2$  = measurement interval length (years) between the 2<sup>nd</sup> and the 3<sup>rd</sup> measurements.

The calculated annual diameter increment was used to obtain the predicted diameter at the second measurement as:

$$DBH_2^* = DBH_1 + DIN * L_1$$

This predicted diameter was then compared with the actual measured diameter to evaluate the assumption of constant annual diameter increment. Four statistics were used for this purpose (n is total number of trees):

- Mean difference =  $\sum_{i=1}^n (DBH_{2i}^* - DBH_{2i}) / n$
- Absolute mean difference =  $(\sum_{i=1}^n |DBH_{2i}^* - DBH_{2i}|) / n$
- Relative mean difference =  $(\sum_{i=1}^n (DBH_{2i}^* - DBH_{2i}) / DBH_{2i}) / n$
- Relative absolute mean difference =  $(\sum_{i=1}^n |DBH_{2i}^* - DBH_{2i}| / DBH_{2i}) / n$

The computed mean difference was 0.1239, absolute mean difference was 0.2944, relative mean difference was 0.0081, and relative absolute mean difference was 0.0221. It is clearly shown that the mean difference and the absolute mean difference between the observed and the predicted diameters are quite small, especially when compared to the magnitude of observed diameters (relative mean difference and relative absolute mean difference). Paired t-test further confirmed that the differences between the predicted and the observed diameters at the 2<sup>nd</sup> measurement are not significant at 95% confidence level. Therefore, it is reasonable to



assume that annual diameter growth rate is constant between two consecutive measurements.

### **Relative diameter increment**

A given amount of diameter increment might not reflect the same survival probability for different sized trees. As a tree grows larger, the non-photosynthetic dry weight increases and the relative growth rate tends to decrease as tree size increases (Buchman et al. 1983). Therefore, the relative diameter increment, the ratio of diameter increment of a tree to its diameter, was considered as another potential predictor variable in addition to diameter increment. This variable was also used to model tree mortality in the Prognosis model (Hamilton 1986).

### **Crown dimensions**

Crown related variables, such as crown width or crown ratio (the ratio of live crown length to total tree height), have been commonly used for growth and mortality modeling (Wykoff et al. 1982, Burkhart et al. 1987, Avila and Burkhart 1992, Zhang et al. 1997, Monserud and Sterba 1999). These variables are good indicators of tree vigor and are preferred whenever possible. Unfortunately, those variables were not measured in the first three measurements in Alberta permanent sample plots and therefore, couldn't be used here. However, as suggested by Monserud and Sterba (1999), one indicator of tree vigor might be enough for mortality modeling. Since diameter increment was already considered, lack of crown related variables was not viewed as a problem for the purpose of mortality modeling.

### **Competition measure**

A major mortality agent is inter-tree competition. The degree of competition greatly influences the survival likelihood of a tree (Dobbertin and Biging 1998). Unless grown openly, a tree always experiences some competition from its neighbors, depending on stand density and the sizes and locations of the neighboring trees. Trees compete for limited physical space and resources such as light, water, and soil nutrients. Some fail the competition and die. Therefore, variables describing this competition are essential for a successful mortality model.

Inter-tree competition can be either one-sided or two-sided. In one-sided competition, larger trees are at competitive advantage over smaller trees, but smaller neighbors do not affect





larger ones. Light is normally the major limiting resource in one-sided competition and competition for light is considered as the primary cause of size inequality and self-thinning in crowded populations (Weiner 1990, Schwinning and Weiner 1997). In two-sided competition, all trees impose some competition on their neighbors, regardless of their sizes. If below ground resources such as water and soil nutrients are also limiting, which might be the case on some sites (e.g., poor sites) or at a certain stage of stand development (Weiner 1990), two-sided competition is expected (Barclay and Layton 1990, Weiner et al. 1997, Kobe and Coates 1997). In addition, large plants have an intrinsic disadvantage because plant growth is sigmoidal, even without competition. Relative growth rate of plants decreases with size and the competitive advantage of large trees are reduced by their intrinsic growth disadvantage (Schwinning and Weiner 1997). Therefore, two-sided competition is also likely to be present. For this study, both types of competition were considered.

Stand basal area is a good measure of stand crowding since it combines both tree size and density. At the same stand development stage, trees in a stand with larger basal area are likely to experience more competition than trees in another stand with a smaller basal area given a regular spacing pattern. Therefore, basal area was considered as a predictor variable in this study to capture two-sided competition.

Competition indices are often used to capture inter-tree competition. Both stand and individual tree level variables can be used to construct competition indices (Mugasha 1989, MacDonald et al. 1990, Salonijs et al. 1991). Most of them are based on easy to measure variables and they are quite simple (Navratil and MacIsaac 1993). However, there are also more complicated competition indices (Brand 1986).

Basal area of larger trees is a commonly used variable to capture one-sided competition and has been used to model growth (Wykoff et al. 1982) and mortality (Monserud and Sterba 1999). It is an individual-tree characteristic and is simply the summation of all the basal areas of trees larger in diameter than the subject tree. For the largest tree in a stand, this variable has the value of zero. This variable was also considered as a potential predictor variable in this study. In mixedwood stands, two types of competition are present: inter-specific competition (competition between trees of different species) and intra-specific competition (competition between trees of the same species). To capture different types of competition, another two



variables were also considered in this study: basal area of larger coniferous trees and basal area of larger broadleaf trees.

Mixedwood stands almost always stratify in height by species due to different height growth patterns and shade tolerant characteristics among species (Larson 1992). In boreal mixedwood stands, the shade intolerant species, aspen, regenerates quickly after major disturbances with rapid juvenile growth and quickly dominates the site and overtop the slow growing, shade tolerant white spruce in the understory (Kabzems et al. 1986). However, aspen height growth will level off around 70 years while long-lived white spruce continues to grow, trying to penetrate the aspen canopy. Spruce leaders may be damaged by wind abrasion during this stage (Thorpe 1992). Eventually, white spruce will take over the dominance (Kabzems et al. 1986). The maximum achievable height for a white spruce tree is about 4 m taller than that for an aspen tree (Vic Lieffers, professor, University of Alberta, personal communication). This is supported by the provincial PSP data set used for this study. The maximum height (the 99<sup>th</sup> percentile of all heights) is 30.6 m for aspen and 34.3 m for white spruce, a difference of 3.7 m.

When competing for light, taller trees have an advantage over their shorter neighbors by casting shade on them. A new variable, basal area of taller trees, was considered capable of capturing this competition and became another potential predictor variable in this study. This variable was calculated similarly as basal area of larger trees except that height was used to determine the competitors for each individual tree.

An intolerant species has a relatively small leaf area index since the lower parts of the crown will be shaded by its own foliage. Shade tolerant species, on the other hand, normally has a larger leaf area index and casts deeper shade on the shorter neighbors (Larson 1992). Therefore, for a shorter tree, the shading by a shade intolerant tree is different from that by a shade tolerant tree. Separation of the competition by shade tolerant group is likely to improve model prediction ability. For this study, two more variables were also considered: basal area of taller shade tolerant trees and basal area of taller shade intolerant trees. Most coniferous species in the PSP data were grouped together as shade tolerant species. However, lodgepole pine was very shade intolerant and was grouped together with all broadleaf species.



## **Species composition**

As discussed in the introduction, species interactions were not well modeled in the old survival functions. Species composition of white spruce was present in the old survival function for aspen. Closer examination revealed that this was the major cause of the large impact of understory white spruce on the survival of overstory aspen. Therefore, white spruce species composition was not used in the new survival function for aspen. On the other hand, a measure of aspen species composition should be in the survival function of white spruce to capture overstory competition. This component was lacking in the old survival function for white spruce. For lodgepole pine, some form of species composition should also be considered to take into account species interactions in mixedwood forests.

## **Site index**

Site index was not used in this study. The survival rates by site classes (good, medium, and poor) using Alberta PSP data did not show any obvious trend. Although there are differences in annual mortality rates for different site classes in Fig. 2.1, they do not produce any clear trend. Site productivity index, another measure of site quality, was used in the old survival functions (see equations (1), (2), and (3)). However, the estimated coefficients had different signs. A positive coefficient was derived for aspen and the coefficients were negative for white spruce and lodgepole pine (Yao et al. 2001). The conflicting signs may indicate that site productivity index is interacting with other variables. Diameter increment is affected by both site quality and competition. Since diameter increment is already considered in this study, it can be used as an indirect measure of site quality. I decided not to include this variable as a predictor variable based on the data and the results shown in the old functions.

### **2.3.2. Model fitting**

Theoretically, both probability of survival and probability of mortality can be modeled. However, it is more convenient to model probability of survival since the survival rate at  $n^{\text{th}}$  year can be calculated directly from the annual survival rate (Vanclay 1995). Therefore, probability of survival was modeled in this study.

As discussed in the introduction, logistic regression appears to be the best method for individual tree mortality modeling and has been widely applied. The majority of mortality models developed using logistic functions are based on data with equal measurement intervals.





Therefore, mortality can be modeled either annually or every  $n$  years with  $n$  equal to the measurement interval (Sterba and Monserud 1999). For data with unequal measurement intervals, annual mortality rate is generally modeled. Mortality rates are either discounted to achieve annual rates (Hamilton 1986) or the measurement length is included in the logistic model, which results in a generalized logistic model (Monserud 1976). Monserud (1976) suggested that having the measurement interval in the exponent gave better results than considering it as another predictor variable.

The data used in this study had unequal measurement intervals that varied from 2.2 to 14.7 years (see Table 2.1). The generalized logistic function with measurement interval in the exponent (Monserud 1976) was adapted in this study to model the annual survival probability of an individual tree:

$$P_s = \left[ \frac{\exp(X\beta)}{1 + \exp(X\beta)} \right]^L = \left[ \frac{1}{1 + 1/\exp(X\beta)} \right]^L = \frac{1}{[1 + \exp(-X\beta)]^L} = [1 + \exp(-X\beta)]^{-L} \quad (4)$$

where

$P_s$  = annual survival probability of an individual tree

$L$  = measurement interval length

$\beta$  = the vector of coefficients

$X$  = the matrix of predictor variables.

All variables identified in Section 2.3.1 were used as potential predictors to fit the generalized logistic function (equation (4)). Although a few statistical methods such as stepwise regression and discriminant analysis exist for variable selection for a logistic function (Peterson and Arbaugh 1986, Wyant et al. 1986), those variables identified as ecologically important were given priorities for inclusion in this study. For each species, the following variables were included as predictor variables: diameter, diameter squared, and diameter increment or the ratio of diameter increment to the diameter of a tree. Diameter and diameter squared were used together to capture the U-shaped mortality trend present in the data. Diameter increment or the ratio of diameter increment to the diameter of a tree was included in the model to represent tree vigor. Besides these variables, various measures of competition were added to the model based on our ecological understanding of competition.



Though a few other methods exist (e.g., non-iterative weighted least squares method and discriminant function analysis method), the maximum likelihood estimator was used for parameter estimations. This estimation method is intuitively appealing and has many desired theoretical properties (Sorenson 1980). For example, it is a consistent and asymptotically efficient estimator. In addition, the probability distribution of the estimator is asymptotically normal (Sorenson 1980). The unknown parameters are estimated in such a way that the probability of obtaining the observed data set is maximized. The iterative reweighted least squares algorithm is usually employed by the maximum likelihood method (Hosmer and Lemeshow 1989, Hogg and Craig 1995). Yao et al. (2001) also applied the maximum likelihood estimation method to estimate the parameters of the old survival functions.

Maximum likelihood estimator is the most commonly used method for estimating parameters of logistic functions and is available in major statistical software packages. S-plus statistical package (Statistical Science 1993) was used in this study for parameter estimation (see Yao 1997 for the S-Plus code). Different starting values were used to ensure that the global maximum, instead of a local maximum, was reached. For a complicated logistic function with many predictor variables, it is quite likely that the function converges to a local maximum.

Many functions were fitted for each species with different predictor variables. The best one was selected for each species based on a goodness-of-fit statistic.

### **2.3.3. Goodness-of-fit test**

All models are imperfect and it is critical to evaluate how well each model performs. The first step in model evaluation is through a goodness-of-fit test.

Goodness-of-fit statistics measure how well a model fits the data used for model development (Hamilton 1986). For continuous response variables, goodness-of-fits of alternative models can be examined by measures like correlation coefficient. However, if the response variable is dichotomous, these measures are not appropriate. Instead, chi-square statistic can be employed as a measure of goodness-of-fit for logistic models with dichotomous response variables (Hamilton and Edwards 1976, Hamilton 1986, Loftsgaarden and Andrews 1992). Fitting data are grouped into several classes based on the independent variable(s). The observed and the expected numbers of surviving or dying trees will be calculated for each class. A chi-square



statistic can then be computed. This calculated chi-square statistic is compared with a critical value from a chi-square table to check if the fitted model is significantly different from the fitting data.

For a model with two or more independent variables, data grouping should be based on all possible combinations of the independent variable values (Loftsgaarden and Andrews 1992). For example, if we have two independent variables and each variable has 10 groups based on all the values of that variable, there will be 100 ( $10 \times 10$ ) groups in total. As the number of independent variables increases, the total number of groups increases sharply. This will result in a large number of groups with fewer observations in each group, sometimes even empty cells. Due to relatively large number of independent variables involved with a wide range of values for each variable, this method is not suitable for this study.

Hosmer and Lemeshow (1989) developed two grouping methods for logistic models with two or more independent variables. Both methods are based on the predicted probabilities from a logistic equation. One method is based on the percentiles of the predicted probabilities. Observations are sorted according to the predicted probabilities and 10 groups are created from these observations with each group comprising 10% of the data, starting from the lowest 10%. It is concluded that the optimal groups for most applications are 10. According to Hosmer and Lemeshow (1989), if group number is too small, we might not be able to detect the difference between observed and estimated frequencies. If the number of groups is less than 6, it is most likely to show that the model fits, even if it does not.

The second method is based on the fixed values of the predicted probabilities. Again, Hosmer and Lemeshow (1989) recommended 10 groups. The first group includes all the observations with predicted probabilities between 0 and 0.1; the second group includes all the observations with predicted probabilities between 0.1 and 0.2; and so on. This grouping method may create unbalanced groups with some groups having large number of observations while others having none or fewer observations. In addition, Hosmer et al. (1988) demonstrated that grouping data based on the percentiles are more close to chi-square distribution and give better results than grouping data based on fixed cut-points.





In this study, Hosmer-Lemeshow's goodness-of-fit statistic was used with the grouping method based on percentiles of the predicted survival probabilities.

The Hosmer-Lemeshow goodness-of-fit statistic is calculated as (Hosmer and Lemeshow 1989):

$$C = \sum_{k=1}^g \frac{(O_k - n_k * \bar{P}_k)^2}{n_k * \bar{P}_k * (1 - \bar{P}_k)} \quad (5)$$

where

$C$  = the Hosmer-Lemeshow goodness-of-fit statistic

$O_k$  = observed number of live trees in class  $k$

$n_k$  = total number of trees in class  $k$

$\bar{P}_k$  = average predicted survival probability in class  $k$

$g$  = total number of groups.

This statistic follows approximately the  $\chi^2$ -distribution with  $(g-2)$  degrees-of-freedom. Detailed description of this statistic can be found in Hosmer and Lemeshow (1989). For each potential logistic function, the Hosmer-Lemeshow statistic was calculated using equation (5) and compared to the critical value with  $(g-2)$  degrees-of-freedom from a  $\chi^2$ -Table. A corresponding  $p$  value can then be derived at 95% confidence level. If a function fits the data well, the  $p$  value associated with that function should be larger than 0.05, indicating no significant difference between the fitted function and the data at 95% confidence level. Several potential functions for each species were compared based on this statistic and the best one with the largest  $p$  value was selected.

#### 2.3.4. Model validation

Based on Hosmer-Lemeshow goodness-of-fit statistic, the best model was selected for each species. However, best fit does not ensure best prediction (Wetherill et al. 1986, Neter et al. 1990). Therefore, prediction statistics were used to further evaluate the selected best functions. If major problems were detected, we would need to go back and refit these functions until satisfactory prediction results were obtained.



Validation data sets described in Section 2.2 were used for model validation. The following two statistics, which can provide almost all the information necessary in model validation (Burk 1986), were used in this study to validate the developed logistic functions:

- Mean deviation =  $\sum_{i=1}^n (Y_i - P_i) / n$
- Mean absolute deviation =  $\sum_{i=1}^n |Y_i - P_i| / n$

where

$Y_i$  = observed survival status of the  $i^{\text{th}}$  tree, with 1 being alive and 0 being dead

$P_i$  = predicted annual survival probability of the  $i^{\text{th}}$  tree

$n$  = number of trees in the validation data set.

For each species, an overall mean deviation and an overall mean absolute deviation were calculated first based on all available data. The validation data were further grouped into several 10 cm diameter classes and these two statistics were computed for each class. This will reveal potential prediction deficiency at certain diameter classes. To compare the prediction accuracy of the old and the new survival functions, the predicted annual survival probability of each tree was calculated using both the old and the new survival functions. Accordingly, the mean deviations and the mean absolute deviations were also given for the old and the new survival functions. These two statistics were also applied by Cao (2000) to validate his mortality model.

Besides these two validation statistics, the observed number of live trees was also compared to the predicted numbers by 10-cm diameter classes created from the validation data set. The predicted number of live trees for each class is simply the summation of the predicted survival probabilities of all the trees in that class. The same method is used in MGM to calculate stand density at each projection step. Both the old and the new survival functions were used to calculate the predicted number of live trees in each diameter class. This allows us to compare the performances of these two sets of functions besides comparing their predictions with the measurement data.



## 2.4. Results

### 2.4.1. Model fitting

Based on Hosmer-Lemeshow goodness-of-fit statistic, the best survival functions for the three species studied are:

$$P_{S-AW} = \left[ 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * GGR * DBH^2)) \right]^{-L} \quad (6)$$

$$P_{S-SW} = \left[ 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * GGR * DBH^2 + \beta_5 * DGGR/BA)) \right]^{-L} \quad (7)$$

$$P_{S-PL} = \left[ 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_6 * GGR + \beta_7 * SC_{PL} + \beta_8 * DBH^2/BA)) \right]^{-L} \quad (8)$$

where

$P_{S-AW}$  = annual survival probability of an aspen tree

$P_{S-SW}$  = annual survival probability of a white spruce tree

$P_{S-PL}$  = annual survival probability of a lodgepole pine tree

DBH = individual tree diameter at breast height (cm)

DIN = annual diameter increment (cm)

GGR = basal area of larger trees (m<sup>2</sup>/ha)

DGGR = basal area of larger broadleaf trees (m<sup>2</sup>/ha)

BA = stand total basal area (m<sup>2</sup>/ha)

$SC_{PL}$  = lodgepole pine species composition, defined as the ratio of lodgepole pine basal area to stand total basal area

L = measurement interval length (yrs)

$\beta_0 \sim \beta_8$  = estimated coefficients.

Equations (6), (7), and (8) are the final survival functions for trembling aspen<sup>1</sup>, white spruce, and lodgepole pine. All the estimated coefficients are listed in Table 2.2. Diameter, diameter squared, and diameter increment are present in all three functions. Basal area of larger trees (GGR) is also a predictor variable in all three functions. However, it is compounded by another variable, diameter squared, in the survival functions for aspen and white spruce ( $GGR * DBH^2$ ). The ratio of basal area of larger broadleaf trees to stand total basal area ( $DGGR/BA$ ) is another predictor variable in the white spruce survival function. For lodgepole

<sup>1</sup> At the final thesis defense, a question was raised that species composition of white spruce might be a good predictor variable for the aspen survival function. Therefore, a new survival function was refitted and presented in Appendix I.





pine, its species composition and the ratio of diameter squared to stand basal area are another two predictor variables in its survival function. Some of the potential predictor variables identified in Section 2.3.1 are not present in these equations because they are not significant at 95% confidence level based on Hosmer-Lemeshow goodness of fit statistic.

#### 2.4.2. Goodness-of-fit test

Table 2.3 presents the Hosmer-Lemeshow goodness-of-fit statistics for the fitting data, and the corresponding p values at 95% confidence level for aspen, white spruce, and lodgepole pine. Ten groups ( $g = 10$  in equation (5)) were used and the groupings were based on percentiles of the predicted survival probabilities. Smaller Hosmer-Lemeshow statistics are associated with larger p values, and vice versa. Large p values indicate that there is no significant difference between observed data and model predictions, which means better fits. All p values in Table 2.3 are larger than 0.05, with the largest one being 0.9118 for aspen, followed by white spruce 0.37125 and lodgepole pine 0.067878. These results suggest that the developed survival functions fit the data well. These equations were further evaluated using validation statistics.

#### 2.4.3. Model validation

Table 2.4 shows the overall mean deviation, the overall mean absolute deviation, and these deviations by diameter classes between the observed and the predicted survival probabilities for all three species based on the validation data. The predicted survival probabilities are calculated using both the new and the old survival functions. For all three species, the overall mean absolute deviations based on the new survival functions are smaller than those based on the old survival functions. When breaking down this statistic by diameter classes, the same conclusion holds with only two exceptions: the smallest diameter classes for aspen and lodgepole pine. Due to high variability in survival rates of smaller trees, this statistic is generally bigger for small diameter classes. The absolute mean deviations in Table 2.4 indicate that all three new survival functions outperformed the old ones.

For white spruce, both the overall mean deviation (-0.0054) and the mean deviations by diameter classes (-0.0795 to -0.0029) are negative using the new survival function, indicating a tendency to overestimate the survival rates. However, all these deviations are very small in absolute magnitude. By using the old function, all these deviations are positive (Table 2.4), showing the trend of underestimation. The absolute magnitudes are much larger than those





calculated from the new function. Therefore, the new function outperforms the old one based on these mean deviations. For lodgepole pine, there is no trend of over- or under-estimation of survival rates using both the old and the new survival functions. However, the new survival function performs better than the old one judged by both overall mean deviations and mean deviations by diameter classes.

For aspen, the mean deviations do not support the better performance from the new survival function. Except for two diameter classes (20-30 and 60-70 cm), the old function gives better results. Therefore, based on this statistic alone, we might conclude that the old function is better than the new one.

Fig. 2.3 shows the observed and the predicted numbers of survival trees by diameter classes. Both the new and the old survival functions are used for calculating the predicted numbers. For all diameter classes of all three species, the numbers of live trees predicted by the new survival functions (PredNew) are closer to the observed ones (Observed) compared to those predicted by the old functions (PredOld), with only one exception for lodgepole pine in the 0-10 cm diameter class. The conclusion also holds when other predictor variables are used for grouping the number of survival trees (graphs not shown). Therefore, we are confident that all three new survival functions perform better than the old ones based on both fitting and validation data sets.

## **2.5. Discussion and conclusions**

Statistical fit is very important in determining whether a growth model is ‘good’ enough. However, it is even more important to evaluate a model’s ecological performances over a wide range of stand conditions. Lack of data in certain stand conditions is frequently the case in forestry. However, it is very important to model these conditions. We need to know how trees grow and die in these conditions and make subsequent management decisions. Compared to automatically selecting predictor variables using a statistical method, fitting a growth model using identified ecologically important predictor variables is a better approach. It is recommended to adopt this approach whenever possible, even at the expense of some statistical properties. If a model is ecologically illogical, it will not perform well for any data set other than the one used for model development (Hamilton 1986).



This study adopted this approach to develop individual tree survival functions for three major tree species in Alberta. Ecologically important variables to tree mortality were identified as potential predictor variables. The developed survival functions outperformed the old ones based on both goodness-of-fit statistics and model validations. All estimated coefficients were consistent with ecological expectations.

From the statistical perspective, some predictor variables are correlated with each other. This phenomenon, commonly referred to as multicollinearity, is particularly likely in growth and yield modeling but can occur in any regression analysis. When predictor variables are correlated, changes in one variable will also lead to changes in the correlated variables. Therefore, care is required when interpreting coefficients associated with correlated variables.

To ensure valid interpretation of the estimated coefficients, the severity of multicollinearity was examined for all survival functions. A condition index was first calculated for each parameter based the eigenvalues of the  $X'X$  matrix with  $X$  being the predictor matrix. The condition index is calculated as the square root of the ratio of the largest eigenvalue to the corresponding eigenvalue of each parameter. The condition number of the predictor matrix  $X$  is defined as the largest condition index. When the condition number is large, the data are said to be ill-conditioned. A condition index of 30 to 100 indicates moderate to strong multicollinearity (see the built in Help for SAS 8.01). For aspen and white spruce survival functions, the condition numbers are quite small (22 for aspen and 18 for spruce). This number is slightly larger for lodgepole pine survival function (34) and it indicates moderate multicollinearity. Examination of the correlations among parameters revealed that for all three species, diameter and diameter squared are highly correlated and therefore, are the major contributors of the calculated condition numbers. Therefore, these two variables should not be interpreted separately. Since the correlations among other variables are quite low ( $r^2 < 0.5$ ), these variables can be interpreted assuming the absence of multicollinearity.

For all three species, the positive coefficients for diameter and the negative coefficients for diameter squared reflected the U-shaped mortality trend (Table 2.2). When trees are very small, they are susceptible to various mortality agents like severe weather conditions, competing vegetation, and animal browsing and trampling. Mortality rates at this stage are very high. Once over this stage, tree mortality rates start to decrease with increasing tree size.



The diameter term dominated the trend over diameter squared when trees are small because of its relatively larger coefficient. As trees continued to grow larger, the diameter-squared increased its impact on increasing mortality rates and eventually took over the dominance. Tree mortality rate started to increase with increasing diameter after that.

Increased mortality rates for large old trees, and therefore the U-shaped mortality trend, are expected. Total photosynthetic surface area (total leaf area) of a stand increases as the stand develops, reaches a maximum level (depending on initial density of the stand), and stabilizes or declines afterwards (Long and Smith 1990, Smith and Long 2001). As pointed out by Smith and Long (2001), the decline in total leaf area might be caused by nutrient limitations. However, it is more likely that mechanical abrasion due to wind is the major factor in limiting leaf area in mature forests. Although the photosynthetic area declines or stabilizes as a stand develops, non-photosynthetic tissues increase continuously. Therefore, the ratio of photosynthetic to non-photosynthetic tissue decreases when trees grow larger. This leads to increased maintenance cost and subsequently less photosynthate available for tree growth. In addition, the net photosynthetic rate per unit leaf area also decreases for old trees (Waring and Schlesinger 1985, Barnes et al. 1998). This is almost certainly related to reduced growth efficiency (amount of stemwood growth divided by leaf area), perhaps resulting from reduced hydraulic conductivity (Ryan et al. 1997, Smith and Long 2001). For example, Long and Smith (1992) reported 60% decline in growth efficiency for lodgepole pine trees between 40 and 120 years.

With increased maintenance cost and reduced photosynthesis, the growth rates of large old trees slow down. As a result, there is not enough photosynthate available to develop resistance chemicals. At this stage, trees are less vigorous, vulnerable to stresses, and susceptible to insect and disease attacks with increased mortality rates.

Diameter increment was also present in the survival functions for all three species. As an indicator of tree vigor, this variable has been frequently used to model tree mortality (Monserud 1976, Buchman et al. 1983, Lorimer 1983, Shugart 1984, Hamilton 1990, Yao et al. 2001). If the diameter increment of a tree is large, it has a better chance of survival as indicated by the positive coefficients for all three species. Normally, stem growth has lower priority of getting the carbohydrates produced from photosynthesis (Waring 1987, Oliver and





Larson 1996, Barnes et al. 1998). After the respiration cost, the remaining carbohydrates are allocated first to leaves and roots, followed by stem growth. Therefore, a tree with a smaller stem growth rate as measured by diameter increment is less vigorous and therefore, has lower survival probability.

Though theoretically promising, the ratio of diameter increment to diameter was not used in this study. This ratio was too big for small trees and it greatly affected the predicted survival probability. This is understandable because trees normally grow fast when they are small. When compared to their small sizes, large ratios are expected. Due to the inclusion of very small trees, this variable was not appropriate. Small trees (diameter less than 2.5 cm) were not included in Prognosis model and using this ratio variable was therefore, not a problem (Hamilton 1986, Hamilton 1990).

Basal area of larger trees (GGR) was a predictor variable for all three species, though the formulation was different. GGR alone with a negative coefficient was present in the survival function for lodgepole pine, which described reduced survival probability when there were more large trees in a stand as measured by a large GGR value. For aspen and white spruce, GGR was compounded by diameter squared and the interaction term  $GGR \cdot DBH^2$  replaced GGR in their survival functions. This new variable also had negative signs and described reduced survival probability with increasing GGR. However, due to the compounding effect from  $DBH^2$ , for a small tree the effect of GGR on survival was less than that for a large tree.

For white spruce, besides the overall impact from all larger trees as measured by GGR, basal area of larger broadleaf trees (DGGR) was also used to predict the survival probability of an individual tree. The ratio of basal area of larger broadleaf trees to stand total basal area (DGGR/BA) was used to capture the competition imposed by broadleaf trees. In typical mixedwood aspen and white spruce stands, white spruce trees stay in the understory of aspen canopy for an extended period before eventually becoming dominant with overstory aspen trees dying out. The ratio variable DGGR/BA measured the relative amount of larger broadleaf trees in the stand and described the competition from these trees. The negative coefficient of this variable indicated decreased survival probability as the broadleaf component increases.



Both basal area of taller trees and basal area of larger diameter trees were considered in this study. However, the majority of trees in the Alberta PSP data set did not have height measurements and they were estimated using an empirical height-diameter relationship for all three species (Huang et al. 1994). Therefore, similar model behavior was observed whether basal area of larger trees or basal area of taller trees was used. For this study, basal area of larger trees and corresponding basal areas by broadleaf and conifers groups were used since they were calculated directly from readily available field measurement data. Basal area of taller trees relied on an empirical height-diameter relationship and might bring in additional prediction errors into the survival functions. It would be interesting to compare the behaviors of these two competition measures when more data with height measurement become available.

Two additional variables, lodgepole pine species composition ( $SC_{PL}$ ) and the ratio of diameter squared to stand total basal area ( $DBH^2/BA$ ), were unique in the survival function for lodgepole pine. The positive coefficient for lodgepole pine species composition indicated better survival probability when there were proportionally more lodgepole pine trees (in terms of basal area) in a stand, i.e., more of a pure lodgepole pine stand. Aspen and black spruce are the two species commonly occurring together with lodgepole pine. When mixed with aspen trees, lodgepole pine trees become easily suppressed by aspen due to their very shade intolerant nature. Therefore, the survival rates of lodgepole pine trees are lower when there are more aspen trees present in a stand. If lodgepole pine trees are mixed together with black spruce, more black spruce trees may indicate wetter sites and associated cold soil might be the cause of reduced survival rates of lodgepole pine trees. The ratio variable  $DBH^2/BA$  had a negative sign and indicated the reduced survival probability with increasing  $DBH^2/BA$ .

The new survival functions developed in this study were incorporated into the Mixedwood Growth Model (MGM) (<http://www.rr.ualberta.ca/research/mgm/mgm.htm>). Although mortality itself is a discrete event (a tree is either alive or dead), stand densities are reduced smoothly in MGM. Each tree simulated/projected represents a certain number of trees on per hectare basis. At each projection step, the survival probability of each tree is multiplied by an expansion factor, the number of trees one projected tree represents when expanded to one hectare. Stand density is simply the summation of the survival probabilities of these trees after multiplication. This method was first applied by Stage (1973) in the well-known growth



model Prognosis.

The developed survival functions outperformed the old ones. However, various MGM simulations still showed problems when extrapolated outside the typical data range used for model development. Unreasonably large stand volumes were detected for stands with high initial densities. Tree mortality rates in these stands were not large enough to bring the densities down to a reasonable level. In addition, short-lived aspen and lodgepole pine stands did not show any sign of breakup even when simulated to very old ages, which is not ecologically reasonable. Lack of data in extreme stand conditions, including very dense stands and very old stands, caused these problems. These extrapolation problems were studied in the next two chapters.

## References

- Alberta Land and Forest Service, 1998. Land and forest service permanent sample plot field procedure manual. Alberta Land and Forest Service, Edmonton, Alberta, 110 p.
- Avila, O.B. and Burkhart, H.E. 1992. Modeling survival of loblolly pine trees in thinned and unthinned plantations. *Can. J. For. Res.*, 22, 1878-1882.
- Barclay, H.J., and Layton, C.R., 1990. Growth and mortality in managed Douglas fir: relation to a competition index. *For. Ecol. Manage.*, 36, 187-204.
- Barnes, B.V., Zak, D.R., Denton, S.R., and Spurr, S.H., 1998. *Forest Ecology*. 4<sup>th</sup> edition, John Wiley & Sons, Inc., 774 p.
- Bella, I.E., 1970. Simulation of growth, yield and management of aspen. Ph.D. thesis, University of British Columbia, Vancouver, 190 p.
- Borders, B.E., Bailey, R.L., and Clutter, M.L., 1987. Forest growth models: parameter estimation using real growth series. *In*: A.R. Ek, S.R. Shifley, and T.E. Burk (eds) *Forest growth modelling and prediction*. pp. 660-667. USDA For. Serv. Gen. Tech. Rep. NC-120.
- Brand, D.G., 1986. A competition index for predicting the vigor of planted Douglas-fir in southwestern British Columbia. *Can. J. For. Res.*, 16 (1), 23-29.
- Buchman, R.G., 1985. Performance of a tree survival model on national forests. *North. J. Appl. For.*, 2, 114-116.
- Buchman, R.G., Pederson, S.P., and Walters, N.R., 1983. A tree survival model with application to species of the Great Lakes region. *Can. J. For. Res.*, 13, 601-608.



- Buchman, R.G., and Lentz, E.L., 1984. More Lake States tree survival predictions. USDA For. Serv. Res. Note, NC-312, 6 p.
- Buford, M.A., and Hafley, W.L., 1985. Probability distributions as models for mortality. For. Sci., 31 (2), 331-341.
- Burk, T.E., 1986. Growth and yield model validation: have you ever met one you liked? *In*: S. Allen and T.C. Cooney (eds). Data management issues in forestry. pp. 35-39. Proc. FORS Computer Symp., Forest Resources Systems Institute, Florence, AL.
- Burkhart, H.E., Farrar, K.D., Amateis, R.L., and Daniels, R.F., 1987. Simulation of individual tree growth and stand development in loblolly pine plantations on cutover, site-prepared areas. Publ. No. FWS-1-87, School of Forestry and Wildlife Resources, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 47 p.
- Cao, Q.V. 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. For. Sci., 46 (1): 127-131.
- Coile, T.S., and Schumacher, F.X., 1964. Soil-site relations, stand structure and yields of slash and loblolly pine plantations in the southern United States. T.S. Coile, Durham, NC, 296p.
- Cunia, T., 1974. Elements of a mathematical framework of statistics. Forest Biometry Monogr Ser., NY State University, Syracuse, NY. Monogr. 1, 163 p.
- Dobbertin, M., and Biging, G.S., 1998. Using the non-parametric classifier CART to model forest tree mortality. For. Sci., 44 (4), 507-516.
- Feduccia, D.P., Dell, T.R., Mann, W.F. Jr., Campbell, T.E., and Polmer, B.H., 1979. Yield of unthinned loblolly pine plantations on cutover sites in the West Gulf Region. USDA For. Serv. Res. Pap., SO-148, 88 p.
- Franklin, J.F., Shugart, H.H., and Harmon, M.E., 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. BioScience, 37 (8), 550-556.
- Goff, F.G., and West, D., 1975. Canopy-understory interaction effect on forest population structure. For. Sci., 21, 98-108.
- Gertner, G., 1987. Approximating precision in simulation projections: an efficient alternative to Monte Carlo methods. For. Sci., 33 (1), 230-239.
- Guan, B.T., and Gertner, G., 1991. Modeling red pine tree survival with an artificial neural network. For., Sci., 37 (5), 1429-1440.
- Hafley, W.L., Smith, W.D., and Buford, M.A., 1982. A new yield prediction model for unthinned loblolly pine plantations. Bioeconomic Modeling Proj. Tech. Rep., 1, Southern Forest Research Centre, School of Forest Resources, NC State Univ., Raleigh, NC, 65 p.





- Hamilton, D.A. Jr., 1974. Event probabilities estimated by regression. USDA For. Serv. Gen. Tech. Rep. INT-152. 9 p.
- Hamilton, D.A. Jr., 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. For. Sci., 32, 989-1000.
- Hamilton, D.A. Jr., 1990. Extending the range of applicability of an individual tree mortality model. Can. J. For. Res., 20, 1212-1218.
- Hamilton, D.A. Jr., and Edwards, B.M. 1976. Modeling the probability of individual tree mortality. USDA For. Serv. Res. Pap. INT-185, 22 p.
- Hann, D.W. 1980. Development and evaluation of an even- and uneven- aged ponderosa pine-Arizona fescue stand simulator. USDA For. Serv. Res. Psp. INT-267, 95 p.
- Harcombe, P.A., 1987. Tree life tables. BioScience, 37 (8), 557-568.
- Harper, J.L., 1977. Population biology of plants. Academic Press, New York, 892 p.
- Hogg, R.V., and Craig, A.T., 1995. Introduction to mathematical statistics. 5<sup>th</sup> edition. Prentice-Hall Inc., Simon & Schuster, Upper Saddle River, New Jersey, 557 p.
- Hosmer, D.W., and Lemeshow, S., 1989. Applied logistic regression. John Wiley & Sons, 309p.
- Hosmer, D.W., and Lemeshow, S., and Klar, J., 1988. Goodness-of-fit testing for multiple logistic regression analysis when the estimated probabilities are small. Biometrical Journal, 30, 911-924.
- Huang, S., 1997. Development of a subregion-based compatible height-site index-age model for black spruce in Alberta. Alberta Land and Forest Service, For. Mgmt. Res. Note No. 5, Pub. No. T/352, Edmonton, Alberta. 55 p.
- Huang, S., Titus, S.J., Lakusta, T.W., and Held, R.J., 1994. Ecologically based individual tree height-diameter models for major Alberta tree species. Alberta Environmental Protection, Land and Forest Services, Forest Management Division. 27 p.
- Hughes, T.P., 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. Am. Nat., 123, 778-795.
- Johnstone, W.D., 1997. The effect of commercial thinning on the growth and yield of lodgepole pine. In: Proceedings of a commercial thinning workshop. pp. 13-23. Whitecourt, Alberta.
- Kabzems, A., Kosowan, A.L., and Harris, W.C., 1986. Mixed section in an ecological perspective. 2<sup>nd</sup> edition. Forestry Division, Saskatchewan Parks and Renewable Resources, Saskatchewan. Tech. Bull. No. 8, 122 p.



- Kelty, M.J., 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. *For. Ecol. Manage.*, 28, 237-257.
- Kirkpatrick, M., 1984. Demographic models based on size, not age, for organisms with indeterminate growth. *Ecology*, 65, 1874-1884.
- Kobe, R.K., and Coates, K.D., 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.*, 27, 227-236.
- Larson, B.C., 1992. Pathways of development in mixed-species stands. *In*: M.J. Kelty, B.C. Larson, and C.D. Oliver (eds). *The ecology and silviculture of mixed-species forests*. pp. 3-10. Kluwer Academic Publishers. Dordrecht, The Netherlands, 287 p.
- Lee, Y.J., 1971. Predicting mortality for even-aged stands of lodgepole pine. *For. Chron.*, 47, 29-32.
- Lenhart, J.D., 1972. Predicting survival of unthinned, old-field loblolly pine plantations. *J. For.*, 70 (12), 754-755.
- Lieffers, V.J., Stadt, K.J., 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. *Can. J. For. Res.*, 24 (6), 1193-1198.
- Loftsgaarden, D.O., and Andrews, P.L., 1992. Constructing and testing logistic regression models for binary data: applications to the National Fire Danger Rating System. USDA For. Serv. Gen. Tech. Rep. INT-286, 36 p.
- Long, J.N., and Smith, F.W., 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. *J. Appl. Ecol.*, 27, 847-856.
- Long, J.N., and Smith, F.W., 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *For. Ecol. Manage.*, 53, 53-64.
- Lorimer, C.G., 1981. Survival and the growth of understory trees in oak forests of the Hudson Highlands, New York. *Can. J. For. Res.*, 11, 689-695.
- Lorimer, C.G., 1983. A test of the accuracy of shade tolerance classifications based on physiognomic and reproductive traits. *Can. J. bot.*, 61, 1595-1598.
- Lorimer, C.G., and Frelich, L.E., 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer saccharum*). *Bull. Torrey Bot. Club* 111, 193-199.
- Lowell, K.E., and Mitchell, R.J. 1987. Stand growth projection: simultaneous estimation growth and mortality using a single probabilistic function. *Can. J. For. Res.* 17: 1466-1470.



- MacDonald, B., Morris, D.M., and Marshall, P.L., 1990. Assessing components of competition indices for young boreal plantations. *Can. J. For. Res.*, 20, 1060-1068.
- Manion, P.D., 1981. *Tree disease concepts*. Englewood Cliffs, Prentice-Hall, 399 p.
- McCune, B., and Cottam, G., 1985. The successional status of a southern Wisconsin oak woods. *Ecology*, 66, 1270-1278.
- Menard, S., 1995. *Applied logistic regression analysis*. Sage Publications Inc., International Educational and Professional Publisher, Thousand Oaks/London/New Delhi, 98 p.
- Monserud, R.A. 1976. Simulation of forest tree mortality. *For. Sci.*, 22, 438-444.
- Monserud, R.A. and Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. *Forest Ecol. Manage.*, 113, 109-123.
- Moser, J.W., 1972. Dynamics of an uneven-aged forest stand. *For. Sci.*, 18, 184-191.
- Mugasha, A.G., 1989. Evaluation of simple competition indices for the prediction of volume increment of young jack pine and trembling aspen trees. *For. Ecol. Manage.*, 26, 227-235.
- Navratil, S., and MacIsaac, D.A., 1993. Competition index for juvenile mixed stands of lodgepole pine and aspen in west-central Alberta. *For. Can., Northwest Reg., For. Cent., Edmonton, Alberta. For. Manage. Note* 57, 8 p.
- Neter, J., and Maynes, E.S., 1970. On the appropriateness of the correlation coefficient with a 0, 1 dependent variable. *J. Am. Stat. Assoc.*, 65, 501-509.
- Neter, J., Wasserman, W., Kutner, M.H., 1990. *Applied linear statistical models*. 3<sup>rd</sup> edn, Irwin, Inc., US, 1181 p.
- Oliver, C.D., and Larson, B.C., 1996. *Forest stand dynamics*. Update edn, John Wiley & Sons, Inc., 520 p.
- Peterson, D.L., and Arbaugh, M.J., 1986. Post-fire survival in Douglas-fir and lodgepole pine: comparing the effects of crown and bole damage. *Can. J. For. Res.*, 16, 1175-1179.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: patterns and process. *Adv. Ecol. Res.*, 27, 213-262.
- Salonius, P.O., Baton, K.P., and Murray, T.S., 1991. How to estimate future competition stress to better spend herbicide dollars. *For. Can., Marit. Reg., Tech. Note* 251.
- Saveland, J.M., and Neuenschwander, L.F., 1990. A signal detection framework to evaluate models of tree mortality following fire damage. *For. Sci.*, 36 (1), 66-76.





- Schwinning, S., and Weiner, J., 1997. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, 113, 447-455.
- Shugart, H.H., 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York, 278 p.
- Silvertown, J.W., 1982. Introduction to plant population ecology. Longman, White Plains, New York, 209 p.
- Smalley, G.W., and Bailey, R.L., 1974. Yield tables and stand structure for loblolly pine plantations in Tennessee, Alabama, and Georgia highlands. USDA For. Serv. Res. Pap., SO-96, 81 p.
- Smith, F.W., and Long, J.N., 2001. Age-related decline in forest growth: an emergent property. *For. Ecol. Manage.*, 144, 175-181.
- Somers, G.L., Oderwald, R.G., Harms, W.R., and Langdon, O.G., 1980. Predicting mortality with a Weibull distribution. *For. Sci.*, 26 (2), 291-300.
- Sorenson, H.W., 1980. Parameter estimation: principles and problems. Control and systems theory, a series of monographs and textbooks, Vol. 9. Marcel Dekker Inc., New York and Basel, 382 p.
- Stage, A.R., 1973. Prognosis model for stand development. USDA For. Serv. Res. Pap. INT-137, 32 p.
- Stage, A.R., and Renner, D.L., 1988. Comparison of yield-forecasting techniques using long-term stand histories. *In*: A.R. Ek, S.R. Shifley, and T.E. Burk (eds), Forest growth and yield modeling and prediction. pp. 810-817. USDA For. Serv., Gen. Tech. Rep. NC-120, Vol. 2.
- Statistical Science, 1993. S-PLUS guide to statistical and mathematical analysis. Version 3.2, StatSci, Seattle.
- Tait, D.E. and Jahraus, K.V. 1988. The contrast in stand dynamics by comparing parameter estimates for a general stand growth model. *Can. J. For. Res.*, 18 (11), 1479-1485.
- Thorpe, J.P., 1992. Patterns of diversity in the boreal forest. *In*: M.J. Kelty, B.C. Larson, and C.D. Oliver (eds). The ecology and silviculture of mixed-species forests. pp. 3-10. Kluwer Academic Publishers. Dordrecht, The Netherlands, 287 p.
- Vanclay, J.K. 1991. Compatible deterministic and stochastic predictions by probabilistic modeling of individual trees. *For. Sci.*, 37, 1656-1663.
- Vanclay, J.K. 1995. Growth models for tropical forests: a synthesis of models and methods. *For. Sci.*, 41 (1): 7-42.



- Walker, S.H., and Duncan, D.B., 1967. Estimation of the probability of an event as a function of several independent variables. *Biometrika*, 54, 167-179.
- Waring, R.H., 1987. Characteristics of trees predisposed to die. *BioScience*, 37 (8), 569-574.
- Waring, R.H., and Schlesinger, W.H., 1985. Forest ecosystems: concepts and management. Academic Press, New York, 340 p.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.*, 5, 360-364.
- Weiner, J., Wright, D.B., and Castro, S., 1997. Symmetry of below-ground competition between *Kochia scoparia* individuals. *Oikos*, 79, 85-91.
- Wetherill, G.B., Duncombe, P., Kenward, M., Kollerstrom, J., Paul, S.R., and Vowden, B.J., 1986. Regression analysis with applications. Chapman & Hall Ltd., London, 311 p.
- Wyant, J.G., Omi, P.N., and Laven, R.D., 1986. Fire induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. *For. Sci.*, 32, 49-59.
- Wykoff, W.R., Crookston, N.L., and Stage, A.R., 1982. User's guide to the stand prognosis model. USDA For. Serv. Gen. Tech. Rep. INT-133, 112 p.
- Yao, X., 1997. Modeling juvenile growth and mortality in mixedwood stands of Alberta. Ph.D. thesis. University of Alberta, Edmonton, Alberta, 193 p.
- Yao, X., Titus, S.J., and MacDonald, S.E., 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. *Can. J. For. Res.*, 31 (2), 283-291.
- Zhang, S., Amateis, R.L., and Burkhart, H.E., 1997. Constraining individual tree diameter increment and survival models for loblolly pine plantations. *For. Sci.*, 43 (3), 414-423.



Table 2.1. Summary of the data used for model development by species and mortality status.

Var.	Live trees					Dead trees				
	N	mean	std	min.	max.	N	mean	std	min.	max.
Trembling aspen										
DBH	11035	22.97	9.49	1.50	72.40	2625	18.26	9.86	1.8	68.10
DIN	11035	0.18	0.11	-0.16	0.89	2625	0.096	0.098	-0.32	0.89
L	11035	8.79	3.64	2.20	14.70	2625	10.03	3.05	2.20	14.70
COBA	11035	14.94	12.90	0.01	56.51	2625	15.39	12.72	0.02	56.83
DEBA	11035	23.91	10.68	0.13	50.48	2625	24.66	10.62	0.19	50.48
BA	11035	35.90	9.64	0.13	62.21	2625	36.60	8.13	0.41	62.21
CGGR	11035	6.41	8.51	0	45.20	2625	8.62	10.46	0	49.96
DGGR	11035	13.89	9.63	0	50.10	2625	19.81	11.18	0	50.40
GGR	11035	20.30	10.85	0	51.00	2625	28.43	10.55	0	54.89
CGGT	11035	5.91	7.66	0	42.26	2625	7.92	9.53	0	42.57
DGGT	11035	13.08	9.55	0	50.10	2625	18.85	11.33	0	50.40
GGT	11035	19.00	10.37	0	50.10	2625	26.77	10.41	0	51.28
SC <sub>AW</sub>	11035	0.34	0.28	0	1.00	2625	0.32	0.29	0	1.00
White spruce										
DBH	9161	19.98	11.01	1.80	72.40	414	15.37	9.51	1.50	49.8
DIN	9161	0.17	0.12	-0.42	0.97	414	0.06	0.09	-0.16	0.67
L	9161	7.90	3.08	2.20	14.70	414	8.58	2.97	2.20	14.70
COBA	9161	32.23	11.72	0.02	58.61	414	34.48	12.45	5.09	55.23
DEBA	9161	8.38	9.57	0	46.86	414	9.11	10.93	0	41.67
BA	9161	40.75	9.14	9.85	62.21	414	43.59	8.35	20.31	62.21
CGGR	9161	22.22	12.59	0	55.28	414	29.32	13.41	0	55.20
DGGR	9161	6.48	8.80	0	46.79	414	8.37	10.67	0	41.67
GGR	9161	28.81	13.39	0	62.17	414	37.69	12.04	0	61.93
CGGT	9161	21.49	12.94	0	55.35	414	28.58	13.78	0	55.22
DGGT	9161	6.19	9.01	0	46.86	414	8.08	10.78	0	41.67
GGT	9161	27.78	14.39	0	62.17	414	36.67	13.29	0	61.93
SC <sub>SW</sub>	9161	0.34	0.31	0	1.00	414	0.36	0.32	0	1.00

(Table 2.1 continued next page)



Table 2.1 (continued). Summary of the data used for model development by species and mortality status.

Lodgepole pine										
DBH	16810	17.20	7.00	1.80	55.90	1666	12.05	5.55	1.80	44.50
DIN	16810	0.13	0.10	-0.36	0.96	1666	0.03	0.06	-0.22	0.57
L	16810	8.87	3.41	2.20	14.70	1666	10.14	2.67	3.00	14.70
COBA	16810	36.18	9.61	0.45	58.60	1666	37.12	8.81	6.23	58.61
DEBA	16810	1.51	4.16	0	36.56	1666	1.20	3.74	0	31.80
BA	16810	36.74	10.34	1.61	62.21	1666	38.05	8.72	3.25	62.21
CGGR	16810	20.62	11.53	0	55.29	1666	30.92	10.28	0	55.43
DGGR	16810	0.85	2.59	0	28.84	1666	0.95	3.04	0	30.82
GGR	16810	21.47	11.54	0	60.12	1666	31.86	9.74	0	61.08
CGGT	16810	20.32	11.38	0	54.55	1666	30.50	10.03	0	54.55
DGGT	16810	0.90	2.74	0	29.87	1666	1.00	3.16	0	31.18
GGT	16810	21.22	11.41	0	60.12	1666	31.49	10.00	0	61.09
SC <sub>PL</sub>	16810	0.41	0.43	0	1.00	1666	0.38	0.42	0	1.00

Note: N is total number of trees; and mean, min., max., and std are mean, minimum, maximum, and standard deviation, respectively.

### Variable description:

#### Individual tree measures:

DBH = breast height diameter (cm)      CGGR = basal area of larger conifer trees (m<sup>2</sup>/ha)  
DIN = annual diameter increment (cm)      DGGR = basal area of larger broadleaf (m<sup>2</sup>/ha)  
L = measurement interval length (yrs)      CGGT = basal area of taller tolerant trees (m<sup>2</sup>/ha)  
GGR = basal area of larger trees (m<sup>2</sup>/ha)      DGGT = basal area of taller intolerant trees (m<sup>2</sup>/ha)  
GGT = basal area of taller trees (m<sup>2</sup>/ha)

#### Stand level measures:

COBA = coniferous basal area (m<sup>2</sup>/ha)      BA = stand total basal area (m<sup>2</sup>/ha)  
DEBA = broadleaf basal area (m<sup>2</sup>/ha)

SC<sub>AW</sub>, SC<sub>SW</sub>, SC<sub>PL</sub> = species composition of aspen, white spruce, and lodgepole pine, defined as the ratio of species basal area to stand total basal area.





Table 2.2. Estimated parameters of all three survival functions.

Variable	Parameter	Parameter estimate		
		Trembling aspen Equation (6)	White spruce Equation (7)	Lodgepole pine Equation (8)
Intercept	$\hat{\beta}_0$	2.198860157	4.029650878	3.92227014
DBH	$\hat{\beta}_1$	0.207354030	0.138378514	0.17237881
DBH <sup>2</sup>	$\hat{\beta}_2$	-0.002858610	-0.001295480	-0.00092726
DIN	$\hat{\beta}_3$	0.659098075	0.416485847	0.39225725
GGR*DBH <sup>2</sup>	$\hat{\beta}_4$	-0.000077809	-0.000079494	
DGGR/BA	$\hat{\beta}_5$		-0.107927052	
GGR	$\hat{\beta}_6$			-0.06646968
SC <sub>PL</sub>	$\hat{\beta}_7$			0.63492435
DBH <sup>2</sup> /BA	$\hat{\beta}_8$			-0.05898038

Note: DBH = individual tree diameter at breast height (cm)  
DIN = diameter increment (cm). Negative values were allowed since trees might shrink a little bit and have negative growth rates.  
GGR = basal area of all larger trees (m<sup>2</sup>/ha)  
DGGR = basal area of larger broadleaf trees (m<sup>2</sup>/ha)  
BA = stand total basal area (m<sup>2</sup>/ha)  
SC<sub>PL</sub> = lodgepole pine species composition  
 $\hat{\beta}_0 \sim \hat{\beta}_8$  = estimated coefficients.

Table 2.3. Overall assessment of the goodness-of-fit of the developed functions.

	Trembling aspen	White spruce	Lodgepole pine
Hosmer-Lemeshow statistic	3.3409	8.666	14.579
P-value	0.91118	0.37125	0.067878



Table 2.4. Mean deviations and mean absolute deviations between the predicted and the observed number of trees using both the new and the old survival functions.

Diameter class	No. of trees	Mean deviation		Mean absolute deviation	
		New	Old	New	Old
Trembling aspen					
0-10	388	-0.2077	-0.1035	0.4848	0.4108
10-20	1951	-0.1171	-0.0102	0.3020	0.3173
20-30	1956	-0.0282	0.0290	0.1710	0.2060
30-40	909	-0.0584	-0.0151	0.1691	0.1910
40-50	207	-0.1103	-0.0513	0.2161	0.2517
50-60	20	-0.2913	-0.1229	0.3618	0.4377
60-70	4	0.1357	0.4169	0.1357	0.4169
overall	5435	-0.0819	-0.0053	0.2425	0.2608
White spruce					
0 -10	2074	-0.0040	0.0393	0.1437	0.1792
10-20	2981	-0.0038	0.0348	0.0899	0.1231
20-30	2322	-0.0069	0.0237	0.0746	0.1021
30-40	1117	-0.0029	0.0381	0.0494	0.0882
40-50	349	-0.0130	0.0532	0.0379	0.1006
50-60	81	-0.0434	0.0659	0.0548	0.1496
60-70	12	-0.0795	0.1116	0.0863	0.2161
overall	8936	-0.0054	0.0345	0.0910	0.1258
Lodgepole pine					
0-10	2167	-0.0131	-0.1160	0.3842	0.3476
10-20	8133	0.0023	-0.0036	0.1630	0.1635
20-30	3530	-0.0016	0.0175	0.0544	0.0728
30-40	550	0.0064	0.0350	0.0277	0.0551
40-50	40	0.0098	0.0393	0.0656	0.0866
50-60	3	0.0088	0.0461	0.0088	0.0416
overall	14423	-0.0008	-0.0137	0.1642	0.1646

Note: the old and the new functions can be found on page 9 and page 26 respectively.



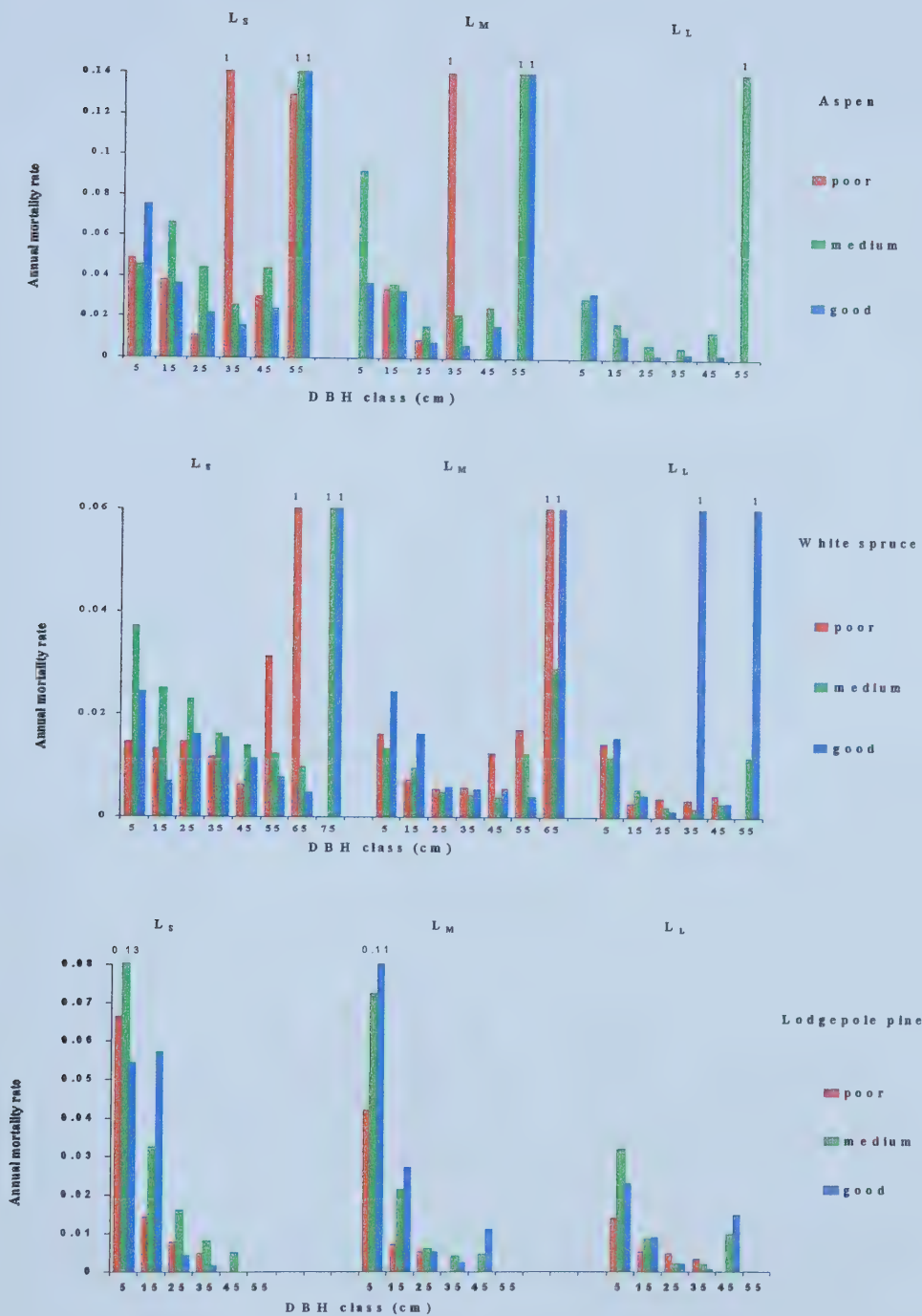


Figure 2.1. Annual mortality rates by measurement intervals (short  $L_S$ , medium  $L_M$ , long  $L_L$ ), site classes (poor, medium, good), and diameter classes.





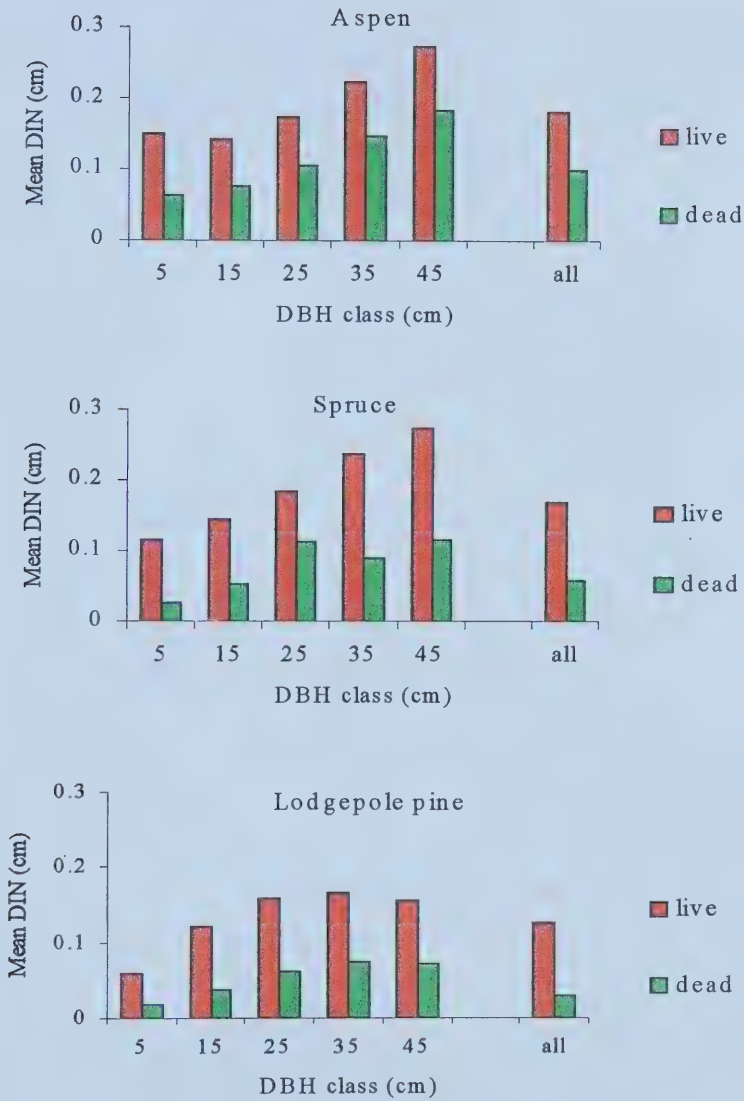


Figure 2.2. Annual diameter increment comparisons between trees that lived and those that died for all three species (labels on DBH classes are midpoint values).



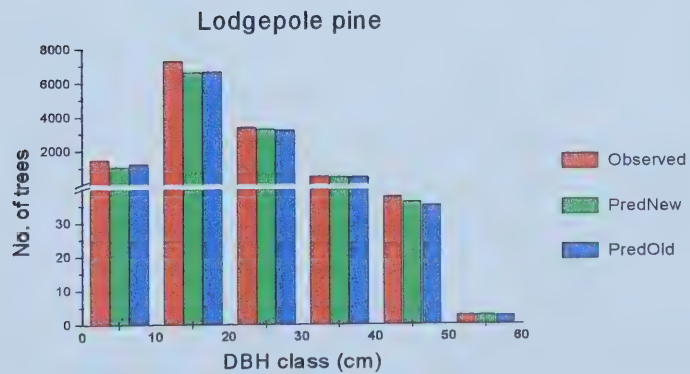
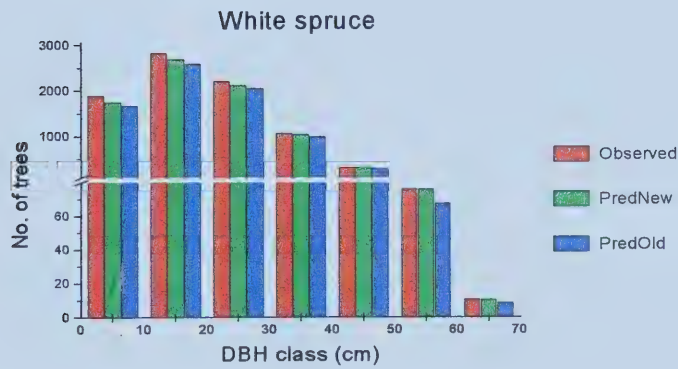
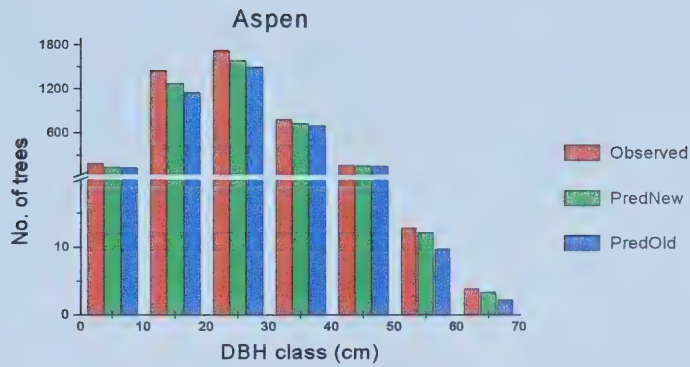


Figure 2.3. Observed (Observed) and predicted numbers of surviving trees using the new survival functions (PredNew) and the old survival functions (PredOld).



## **Chapter 3. Maximum size-density relationship for constraining individual tree mortality functions<sup>1</sup>**

### **3.1. Introduction**

Mortality modeling is a key component of growth and yield modeling. During the last few decades, many mortality models, some at the stand level, and others at the tree level, have been developed for different stand types and tree species. Stand level mortality models predict stand density changes over time, while individual tree mortality models predict the probability of survival or death for each individual tree involved in growth projections. To make better management decisions, we need not only the number of dead trees, but also the sizes and the species of these trees. Individual tree models, though more complicated, can provide such information and are often preferred from a management perspective, especially for intensive forest management (Vanclay 1994).

However, because of the cumulative errors resulting from growth projections, individual tree models may not be accurate for stand level predictions (Zhang et al. 1997). Cumulative errors occur when stand level variables are calculated using several individual tree growth equations. Each equation will have a prediction error and these errors will be accumulated into stand level predictions. Cumulative errors may also occur in iterative (multiyear projection) models. After the first iteration, prediction errors will accumulate through the projection system because errors propagate (Gertner 1987). To achieve compatibility, several methods have been developed (Clutter 1963, Burkhardt and Sprinz 1984, McTague and Bailey 1987, Daniels and Burkhardt 1988). Among these methods, simultaneous regression techniques, which are commonly used in econometrics, have been applied in forest growth and yield modeling (Borders 1989, LeMay 1990, Huang 1992, Lynch and Murphy 1995).

However, most of those studies are for models of the same resolution. Zhang et al. (1997) developed a simultaneous estimation approach to ensure compatibility between stand level and individual tree level models. A seemingly unrelated equation system was formed using the

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<sup>1</sup> A version of this chapter has been accepted by Forest Ecology and Management (In press).



individual tree mortality model (a logistic function) and the number of trees in each diameter class. The estimated parameters of the individual tree mortality model were constrained by the number of trees in each diameter class and therefore, are compatible with stand level measures of density changes. However, the mortality model was not improved and the authors argued that limited mortality data were responsible for the lack of improvement. A special algorithm was developed for parameter estimation because there was no existing method for estimating parameters of a simultaneous equation system involving logistic functions.

To improve stand level predictions of the individual tree mortality functions developed in Chapter 2, this study was aimed at developing a maximum size-density relationship to be used as a theoretical constraint on the existing individual tree mortality model. The concepts of the self-thinning rule (Yoda et al. 1963) and Reineke's stand density index (Reineke 1933) were used here. The maximum size-density relationship was based on the data for all species and all site qualities. However, the influences of species and site quality were investigated.

## **3.2. Materials and methods**

### **3.2.1. The data**

The data used for this study were the permanent sample plot (PSP) data collected by Alberta Land and Forest Service over the last 40 years throughout the forested area of the province of Alberta. The data were from 699 locations and covered wide ranges of ages, stand densities, species compositions, and site conditions in the province. At each of the 352 locations there was a cluster of 4 plots, while there was only one plot at each of the remaining 347 locations. Detailed information can be found in the permanent sample plot field procedure manual (Alberta Land and Forest Service 1998).

There were 1755 plots in total with up to six re-measurements of individual tree characteristics. For each plot, quadratic mean diameter, stand basal area, stand density (number of stems per hectare), and species composition were calculated at each measurement for each major species considered separately and for all species combined (except species composition). Species composition was calculated as the ratio of species basal area to stand total basal area. Given available stem analysis data, site index at 50 years breast height age was also calculated for each species in each plot using the models developed by Huang (1997) and Huang et al. (1997a, 1997b). Three major species were considered: trembling aspen





(*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm). Table 3.1 presents a summary of these stand level variables.

All available plot data were grouped into density classes of 100 trees per hectare. If there were more than five data points in a density class, the first five stands with the largest quadratic mean diameters were selected to develop the maximum size-density relationship. About 70% of the data were randomly selected for model fitting using the random number generating function RANUNI in SAS (SAS Institute Inc. 1985). The remaining 30% of the data were used for model validation.

### 3.2.2. Model selection

The concepts of the self-thinning rule and Reineke's stand density index were used here. The self-thinning rule was first proposed by Tadaki and Shidei (1959) and first generalized by Yoda et al. (1963). It began as an empirical relationship between the maximum achievable average plant weight ( $w$ ) and the number of plants per unit area ( $N$ ) in an even-aged, pure-species population with complete crown closure. When plotted on a log-log scale, the relationship follows a straight line, the commonly called 'self-thinning line':

$$\ln w = -1.5 \ln N + k_1 \quad (1)$$

If total plant weight per unit area ( $W$ ) is used as dependent variable, the self-thinning line becomes:

$$\ln W = -0.5 \ln N + k_2 \quad (1a)$$

where  $k_1$  and  $k_2$  are constants.

Though initiated for pure species even-aged stands, the self-thinning rule was also demonstrated applicable to mixed species populations (Bazzaz and Haper 1976, Malmberg and Smith 1982, Westoby 1984, Solomon and Zhang 1998, Sturtevant et al. 1998, Wilson et al. 1999).

Reineke (1933) stated that in an even-aged monospecific stand with complete crown closure, the maximum attainable number of trees per unit area ( $N$ ) was negatively correlated with the quadratic mean diameter ( $D$ ). This relationship follows a straight line when plotted on log-log scale:



$$\ln N = -1.605 * \ln D + p \quad (2)$$

Equation (2) can be expressed in an analogous way to the self-thinning line:

$$\ln D = -0.623 * \ln N + q \quad (2a)$$

where  $p$  and  $q$  are constants.

Reineke's stand density index and the self-thinning rule are essentially the same in that both are used to define a maximum stand density at a given stand average size. However, different variables are used to represent stand average size. Average plant weight is used in the self-thinning rule, while stand quadratic mean diameter is used in Reineke's stand density index. When average plant weight is used, it is assumed that all trees of the same species have similar geometrical shape regardless of growth stage and habitat conditions. As pointed out by Yoda et al. (1963), this assumption is not required if average diameter ( $D$ ) is used because stem diameter is usually measured at a fixed height regardless of tree size. They argued that if this assumption is true, the plant weight should be proportional to  $D^3$ . However, the weight of a tree is proportional to  $D^{2.5}$  in most cases (Yoda et al. 1963). In addition, stand density is the independent variable in the self-thinning rule, but it is the dependent variable in Reineke's equation.

Various attributes, such as tree diameter, stem weight or volume, crown width, crown projected area, or leaf area per tree, can be used as average tree size in a self-thinning relationship (Jack and Long 1996). Crown width is a major factor affecting the degree of stand density and crown closure (Jack and Long 1996). Compared to stem volume or weight, diameter is better correlated with crown width (Zeide 1987, Hynynen 1993). In addition, diameter is the most easily measured tree attribute and is less subject to measurement errors. Quadratic mean diameter was chosen to represent average tree size for developing the maximum size-density relationship in this study.

Zeide (1987) argued that the self-thinning line is not a straight line, but a curve concave downward. Preliminary analysis of our data also showed a curvature trend between quadratic mean diameter and stand density when plotted on a log-log scale. At the middle range of stand densities, a straight line was able to approximate the relationship between quadratic mean diameter and stand density with both variables in log scales. However, for stands with low and high densities, the data points were well below the straight line. It was, therefore, not



appropriate to describe this relationship using a straight line. Subsequently, it was not necessary to use the log-transformed data. For this study, the original data were used to fit the maximum size-density relationship between quadratic mean diameter and stand density. Plotting of quadratic mean diameters against stand densities showed a reversed J-shaped trend.

A universally fixed slope was assumed for the self-thinning line when it was first developed (Reineke 1933, Yoda et al. 1963). However, various studies (Zeide 1987, Hynynen 1993) showed that the self-thinning line was affected by species and sometimes site quality. In fact, Zeide (1987) argued that the self-thinning line did not have any constant slope, but changed according to the stage of stand development. In this study, all the data selected for model fitting were used to develop the maximum size-density relationship between quadratic mean diameter and stand density. The effect of site quality and species were examined later.

Five potential functions were selected as candidate functions and they are listed in Table 3.2. Detailed information about these five functions can be found in Ratkowsky (1990). These are all concave curves. Functions (1) and (2) are two parameter models, while functions (3), (4) and (5) are three parameter models. The log-log transformation of function (1) is a straight line and it has the same functional form as equation (2a). Function (2) is known as the typical reciprocal model in yield-density studies in agricultural research. Function (4) has also been proposed for use in yield-density studies (Ratkowsky 1990). These five functions were selected from many reversed J-shaped curved listed by Ratkowsky (1990) based on preliminary regression analysis.

The average size-density relationship was fitted first for each of the five functions for model selection. Based on the fitting data set, the parameters of each function were estimated using the Gauss-Newton method for nonlinear regression in SAS/STAT software (SAS Institute Inc. 1989). Though the log-log transformation of function (1) is linear, it was still estimated as a nonlinear regression to avoid the lognormal bias (Flewelling and Pienaar 1981, Miller 1984).

Model (1) was linearized and the estimated coefficients were used as the initial values for nonlinear regression. For other functions, the selected model fitting data were used to pick up initial values. For example, for function (2), by visually checking the scatter plot between quadratic mean diameter and density, quadratic mean diameter is about 50 when density is





zero. Therefore, parameter  $a$  takes its initial value of 0.02 as calculated by function (2). Another data point was used to get the initial value for the parameter  $b$  based on the same rationale. A similar method was used to pick initial values for parameters in other functions. Various initial values were also used to fit the functions in an attempt to avoid a local minimum.

For each function, the mean squared error of the fit and the scatter plot of studentized residuals against predicted quadratic mean diameters were used to judge the goodness of fit. Studentized residuals were used in an attempt to overcome the dependence among ordinary residuals (Neter et al. 1990).

### 3.2.3. Model validation

Prediction statistics, instead of fitting statistics, should be used for final model selection because best fit does not mean best prediction (Wetherill et al. 1986, Neter et al. 1990). There are many model validation methods, but none of them is universally good. Several methods should be applied in order to evaluate the fitted functions thoroughly. The following six commonly used prediction statistics (Wang et al. 1998, Huang et al. 1999) were used to evaluate the five fitted functions using the validation data set:

- Mean prediction bias:  $\bar{e} = \frac{\sum_{i=1}^n (QMD_i - \hat{QMD}_i)}{n} = \frac{\sum_{i=1}^n e_i}{n}$
- Standard deviation of the prediction bias:  $std = \sqrt{\frac{\sum_{i=1}^n (e_i - \bar{e})^2}{n - 1}}$
- Percent bias:  $\bar{e}\% = \frac{\bar{e}}{\overline{QMD}} \times 100 = \frac{\bar{e}}{\sum_{i=1}^n QMD_i / n} \times 100$
- Mean squared error of prediction:  $MSEP = \frac{\sum_{i=1}^n (QMD_i - \hat{QMD}_i)^2}{n}$
- Relative error in prediction:  $RE\% = \frac{\sqrt{MSEP}}{\overline{QMD}} \times 100$



- Coefficient of determination:  $R^2 = 1 - \frac{\sum_{i=1}^n (QMD_i - \hat{QMD}_i)^2}{\sum_{i=1}^n (QMD_i - \overline{QMD})^2}$

where  $n$  is the sample size of the validation data set;  $QMD_i$  is the quadratic mean diameter of the  $i^{th}$  case;  $\hat{QMD}_i$  is the predicted quadratic mean diameter of the  $i^{th}$  case;  $\overline{QMD} = (\sum_{i=1}^n QMD_i / n)$  is the average quadratic mean diameter; and  $e_i = (QMD_i - \hat{QMD}_i)$  is the prediction error of the  $i^{th}$  case.

Both mean prediction bias and percent bias give an average measure of the differences between the predicted and the observed quadratic mean diameters, with mean prediction bias in absolute terms and percent bias in relative terms. Standard deviation of the prediction bias measures the spread of prediction errors (precision). MSEP incorporates both bias and variation and is a better measure on the performance of a model. RE% is just another expression of MSEP in a relative scale. The variation in the validation data set explained by each fitted function is given by  $R^2$ . Higher  $R^2$  and smaller MSEP, RE%,  $\bar{e}$ ,  $\bar{e}\%$ , and std values indicate a better model for prediction.

Besides the prediction statistics described above, two types of plots were also used to evaluate the five fitted functions on their prediction abilities:

- Plot of prediction biases against predicted quadratic mean diameters
- Plot of observed against predicted quadratic mean diameters.

With these model validation methods, one or more models of the average size-density relationships were selected as the final model(s) for further analysis.

### 3.2.4. Maximum size-density relationship

To derive the maximum size-density relationship, a technique developed by Smith and Woods (1997) was used. The model fitting data set and the model validation data set were pooled together for this purpose. The final model(s) selected through model validation were used to derive the maximum size-density relationship. A loss function was used to refit the final



model(s) using the nonlinear regression technique (Gauss-Newton method). For each density class (100 trees/ha), the data point with the highest quadratic mean diameter was selected and its quadratic mean diameter was defined as the maximum quadratic mean diameter for that density class. During the parameter estimation process, ‘the loss’ was defined as the difference between the estimated quadratic mean diameter of a density class and the maximum quadratic mean diameter of that density class. If ‘the loss’ was negative, a value of 20 was added to the estimated quadratic mean diameter to ‘shift’ the fitted line up. The objective of introducing the loss function was to ensure that the fitted curve was above the majority of the data points and therefore, defined the maximum size-density relationship. With this technique, one final model was selected as the best maximum size-density curve for constraining the empirical individual tree mortality model in MGM.

The derived maximum size-density relationship was for all species and all sites combined. This was based on the assumption that neither species nor site quality affected the self-thinning line in mixedwood stands. However, some researchers (e.g., Puettmann, et al. 1993 and Hynynen 1993) argued that the self-thinning line was affected by species and/or site quality. Either the intercept was lower, or the slope was flatter for very poor sites. Westoby (1984) thought that some species grew in different shapes (different crown structure) on different sites, while other species simply grew faster or slower on different sites.

The effects of site quality and species on the derived maximum size-density relationship were investigated in this study. Species quadratic mean diameter (SPQMD) was calculated as

$$SPQMD = 200 \times \sqrt{\frac{SPTOTBA}{\pi \times SPTOTDEN}}$$
; where SPTOTBA is species total basal area (m<sup>2</sup>/ha) and SPTOTDEN is species total density (stems/ha).

This calculation was done for each of the three major species involved, i.e., trembling aspen, white spruce, and lodgepole pine. A linear regression model of total stand density (DEN) against species quadratic mean diameter (SPQMD) in logarithmic scale was fitted for each species and for all species combined as:

$$\ln DEN = a + b \cdot \ln SPQMD \quad (3)$$



Equation (3) was purposely fitted with stand density as the dependent variable and species quadratic mean diameter as the independent variable for the convenience of comparing the results with Reineke's equation (2). This was different from fitting the five average size-density equations where quadratic mean diameter was the dependent variable. The purpose here was to compare the estimated slope coefficient for each species with Reineke's constant slope to determine if the developed maximum size-density relationship was separable by species.

A site productivity measure was calculated by averaging the site indices of all species in each permanent sample plot. This gave an overall indication of how good a site was for the mixed stands, i.e., the productivity of a site for all species together, not for each individual species. The data set was split into three subsets according to the calculated site productivity values: one for poor sites (productivity < 12), one for medium sites ( $12 \leq \text{productivity} \leq 16$ ), and one for good sites (productivity > 16). Grouping of the calculated site productivity values into a few classes allows us to fit separate maximum size-density curves and evaluate the impact of site quality on the maximum curve. For this study, the final selected maximum size-density relationship was fitted to each of the three data sets. A visual comparison of the differences among these three curves was done first by overlaying them on top of each other. The Kolmogorov-Smirnov test (Steel et al. 1997) was then performed to detect any significant difference between each of the three curves with the overall curve for all species.

The basic principle of the Kolmogorov-Smirnov test is to rank all the observations from two populations; determine the sample cumulative distribution functions  $F_1(Y_1)$  and  $F_2(Y_2)$ ; and calculate the maximum difference between these two populations by  $D = \max [F_1(Y_1) - F_2(Y_2)]$ . This maximum difference will be compared with a critical value from a Kolmogorov-Smirnov table at a given  $\alpha$  level and given sample sizes of both populations. If the calculated Kolmogorov-Smirnov statistic is smaller than the critical value, then the null hypothesis will be accepted, which indicates no significant difference between the two populations (Steel et al. 1997). Each of the three fitted curves for the three site productivity classes and the overall curve for all sites were used to predict quadratic mean diameters for varying stand densities. This resulted in four populations. We then compared the results of each of the three site productivity classes with the overall model to detect any significant difference using Kolmogorov-Smirnov test.





### 3.3. Results

Table 3.3 gives the estimated coefficients and the mean squared error for each function listed in Table 3.2 based on the model fitting data. Fig.3.1 shows the fitted models overlaid with the data and Fig.3.2 shows the studentized residuals plotted against the predicted quadratic mean diameters. Model (4) appears to be the best with the smallest mean squared error (0.8713) and the residuals are randomly distributed (Fig. 3.2d). The overlaid plot in Fig. 3.1d also suggests a good fit for model (4). Figs. 3.1e and 3.2e indicate that model (5) is also good, with a slightly larger mean squared error (1.0123). The mean squared errors are quite big for models (1) and (3). The obvious bad fitting is shown in Figs. 3.1a, 3.2a, 3.1c, and 3.2c. Model (1) underestimates the quadratic mean diameters at lower densities and overestimates them at higher densities (Figs. 3.1a and 3.2a). The quadratic mean diameters are overestimated at lower densities and underestimated at higher densities by model (3) (Figs. 3.1c and 3.2c). The curvature trends in Figs. 3.2a and 3.2c also confirm the bad fitting for model (1) and model (3). Though the mean squared error is not too big, model (2) is not considered for further analysis because there is also a curvature trend in the residual plot (Fig. 3.2b), which indicates a biased fit.

Based on the validation data set, the calculated prediction statistics for all five models are listed in Table 3.4; the prediction biases against the predicted quadratic mean diameters are plotted in Fig. 3.3; and the observed against the predicted quadratic mean diameter plots are given in Fig. 3.4. These results show that model (4) and (5) are equally good for prediction. Model (4) has smaller MSE<sub>P</sub>, RE%, and higher  $R^2$ , but model (5) has smaller  $\bar{e}$  and  $\bar{e}\%$ . The differences in these prediction statistics are very small between model (4) and model (5). The prediction biases are random and small for both models (Figs.3.3d and 3.3e) and the predicted quadratic mean diameters are well correlated with the observed ones for both models (Figs.3.4d and 3.4e).

Based on the results of model fitting and model validation, model (4) and model (5) were selected as the candidate models for the maximum size-density curve fitting. With the defined loss function, the fitted maximum size-density functions were:



$$QMD = \frac{1}{0.0078891809 + 0.0003913343 \times DEN^{0.6097905851}} \quad (4)$$

$$QMD = 5.20973 \times \exp\left(\frac{7031.84227}{DEN + 3156.06012}\right) \quad (5)$$

where QMD is quadratic mean diameter and DEN is stand total density.

These two fitted models are shown in Fig. 3.5 and Fig. 3.6. The two models perform similarly at the middle range of the data. However, model (4) (equation (4)) behaves better at extreme densities, especially at very high densities. Quadratic mean diameter continues to decrease as density increases towards infinity for model (4). However, with model (5) (equation (5)), quadratic mean diameter approaches an asymptote (5.20973) as density approaches infinity, which is not realistic. We expect quadratic mean diameter to decrease as density increases, even at extreme high densities. When density decreases towards zero, both models cross the vertical axis. Nevertheless, model (5) crosses the vertical axis faster (at QMD = 48.355 cm). This means that the model can not be used on any stand with quadratic mean diameter greater than 48.355 cm. Therefore, model (4), which crosses the vertical axis at quadratic mean diameter 127.756 cm, is chosen to be the final model for constraining the empirical mortality functions.

For each species, the straight-line fit of stand total density as a function of quadratic mean diameter in log-log scale (equation (3)) was obtained and results are presented in Table 3.5. The coefficients of determination are very low, indicating very weak linear relationships. If Reineke's line works for each individual species in mixedwood stands, the slope coefficients should be around -1.605. However, the estimated slopes are quite different for the three species and they are far from Reineke's slope -1.605. When all species are combined together, the slope coefficient (-1.6869) is close to Reineke's slope. This result supports Westoby's (1984) conclusion that in mixed species stands, the self-thinning rule only works for all species taken as a whole, not for each individual species. The relationship between species quadratic mean diameter and total stand density in original scale showed too much variation and a maximum size-density relationship could not be developed for each individual species. Therefore, separation of the maximum size-density relationship by species is not possible. As a result, the developed maximum size-density relationship will be used to constrain all three empirical mortality functions developed in Chapter 2. In mixedwood stands, this maximum



size-density relationship will serve as a single upper limit for constraining the empirical mortality functions in MGM.

The coefficients of the three curves (based on model (4)) fitted separately for three site productivity classes are given in Table 3.6. The results for productivity classes do not differ much. A plot of these three curves did not show any deviation from each other (graph not shown). This was confirmed by the Kolmogorov-Smirnov test. Both visual comparison and the Kolmogorov-Smirnov test indicated that site quality did not affect the maximum size-density relationship. This was supported by many studies (e.g., Yoda, et. al. 1963, White and Harper 1970, and White 1980), i.e., the relation of mortality to biomass accumulation is considered the same for all sites. Stands on good sites thin along the same trajectory as those on poorer sites. However, biomass accumulates faster on good sites because trees grow faster. Therefore, trees die faster on good sites.

### 3.4. MGM implementation

The maximum size-density relationship developed in this study is incorporated into MGM as a theoretical constraint on the empirical survival functions. Since it is not separable by species, the same upper limit is used for each individual species and for both pure and mixed species stands. At each growth projection in MGM, both stand quadratic mean diameter (QMD) and stand density (DEN) are calculated. The maximum allowable density for the calculated quadratic mean diameter can then be computed by reformulating equation (4):

$$DEN_{\max} = \left( \frac{1/QMD - 0.0078891809}{0.0003913343} \right)^{\frac{1}{0.6097905851}} \quad (6)$$

If the calculated stand density (DEN) exceeds the maximum allowable density, a reduction factor on the survival probability of each individual tree will then be calculated:

$$F = \begin{cases} \left( \frac{DEN_{\max}}{DEN} * \frac{DBH}{DBH_{sp\max}} \right)^{0.2} & (\text{if } DEN > DEN_{\max}) \\ 1 & (\text{if } DEN \leq DEN_{\max}) \end{cases} \quad (7)$$

In equation (7), the exponent 0.2 is used to bring the stand back onto or below the maximum size-density line in less than 5 years, depending on the size distribution of individual trees. The ratio of individual tree diameter (DBH) to the maximum diameter of the species ( $DBH_{sp\max}$ ) that tree belongs to is used to account for tree size differences. According to the self-thinning theory, smaller trees have higher mortality rates in a crowded stand. In a pure





species stand, species maximum diameter is identical to the maximum diameter of the stand. In mixed species stands like the typical aspen and white spruce mixtures, the relative position of an individual tree is considered within its own species. For example, in a mixedwood stand of aspen and white spruce, each aspen tree is compared to the largest aspen tree to define its relative position. Accordingly, each white spruce tree is compared to largest white spruce tree in the stand to define its relative position. Equation (7) will then be used to determine the reduction factor for each individual aspen or white spruce tree.

Equation (7) shows that for a given tree, the larger the projected stand density is compared to the maximum allowable density, the smaller the factor  $F$  is, and therefore the faster trees should die to bring the stand back onto the maximum size-density line. On the other hand, at a given stand density, the smaller an individual tree is compared to the largest tree of the same species in the stand, the smaller the factor  $F$  is.

The reduction factor  $F$  is bounded between 0 and 1. It will be multiplied by the probability of survival ( $P_s$ ) of an individual tree calculated from the empirical survival functions to derive the final survival probability of that tree:

$$P_{s_i} = P_s * F \quad (8)$$

As stand growth projection continues, once the projected stand density exceeds the maximum allowable density calculated from equation (6), equation (8) will be activated to reduce the survival rate of each individual tree and bring stand density back onto the maximum size-density curve.

### 3.5. Discussion and Conclusions

The self-thinning rule has often been employed in modeling density-related mortality (Mitchell 1975) and in forest management using stand density management diagrams for both single species stands (Drew and Flewelling 1977, 1979, McCarter and Long 1986) and mixedwood stands (Sturtevant et al. 1998, Wilson et al. 1999). According to the self-thinning rule, a population of plants in a given environment can occupy any point below the maximum size-density line but cannot exceed it. At the limit, growth of large, dominant plants drive the mortality of small, suppressed plants.



Mortality data are relatively rare, even if we have a large body of measurement data, since long time spans are needed to capture dead trees. In addition, in the PSP data set used in this study, there are no data on stands with extreme stand conditions because of the typical plot selection procedures. Therefore, when extrapolated, the empirical functions do not guarantee reasonable model predictions. A stand may exceed the maximum size-density line as growth projection continues. With the derived maximum size-density curve, the empirical mortality functions can be constrained. For a given stand, its quadratic mean diameter and density can be calculated easily at any time during growth projections. If the combination of this quadratic mean diameter and density exceeds the maximum size-density line, trees are forced to die quickly and maintain the stand on or below the maximum size-density curve. This methodology has great potential in constraining other types of mortality functions and for other species in other regions.

Due to the complexity of mortality process and the uncertainty in the timing of tree death, mortality remains one of the least understood components of growth and yield estimation. Stage and Renner (1988) found that most (80%) of the variability in volume predictions for mixed conifer forests in the Rocky Mountains region (US) was due to the uncertainty in mortality estimates. Similar problems were reported through growth and yield comparisons using MGM.

The primary application of the maximum size-density relationship developed in this study is to constrain the empirical mortality functions in MGM. This relationship is based on the well-accepted ecological theory and is very easy to implement. In addition, it is developed independent of the mortality model that needs to be constrained. This has the advantage of modifying any mortality function without changing this relationship.

Due to lack of data and highly variable tree mortality in very young and very old stands, mortality predictions are often less accurate in these stands, even very poor sometimes. It is therefore important that the developed maximum size-density relationship can provide reasonable constraints at these extremes. It may not be appropriate theoretically to extrapolate either the self-thinning line or Reineke's line to these two extremes. Both theories are based on competition related mortality only. However, competition related mortality does not occur throughout the life span of a stand. For a newly regenerated stand, especially when its density



is low, the site is not fully occupied. There are plenty of resources available and trees do not compete with each other. Tree mortality at this stage is caused by other mortality agents like severe weather conditions or animal browsing (Yao 1997). As trees continue to grow larger, self-thinning begins and trees start to compete with each other for limited growing space and resources such as light, water, and mineral nutrients (Westoby 1984). As the stand continues to develop, competition related mortality diminishes at some advanced age. Beyond that age, tree mortality is independent of competition again (Lloyd and Harms 1986). Therefore, the self-thinning rule and Reineke's stand density index are not applicable at the two extremes of stand development. This might be the reason why a curvature trend has been detected in some studies, including this study, at the two ends in the linear self-thinning line.

The developed maximum size-density relationship in this study did not differentiate competition induced mortality from mortality caused by other agents. All stands with largest quadratic mean diameters for a given density class were used to develop this relationship and therefore, can be used as an upper limit for any stage of stand development. With this theoretical constraint, the accuracy in stand density projections can be improved and therefore, the variability in volume estimations caused by mortality functions can be reduced.

Site quality did not influence the maximum size-density relationship. This confirms the basic assumption of the self-thinning concept. Trees grow faster and accumulate biomass faster on good sites. But the self-thinning trajectory is the same as that on poor sites and therefore, the maximum quadratic mean diameter for a stand is fixed at a given stand density.

Although the self-thinning rule worked separately for each individual species in some mixed species populations (Bazzaz and Haper 1976; Malmberg and Smith 1982), this might only be true for mixed species populations with very simple structure. There were only two species involved in Bazzaz and Haper's and Malmberg and Smith's studies and they were in equal proportions. In addition, both species were planted at the same time and individual plant locations were well controlled in the greenhouse. Even so, the slopes of the two species in Malmberg and Smith's study are quite different from each other (-1.63 versus -1.41). They also differ from the slope of all the data combined (-1.75). Therefore, they are not really very close as interpreted by the authors. In fact, Westoby (1984) examined the above-mentioned papers and concluded that although the self-thinning rule worked for mixed species stands, it





only applied to mixed species stands taken as a whole, not to each species considered separately.

Unlike the well-controlled simple mixtures discussed above, both vertical and horizontal structures are much more complex in mixedwood forests, especially for uneven-aged stands. A particular species may develop a completely different role in different types of mixtures. Therefore, for a particular species, data from various mixtures are not able to produce a reliable self-thinning line. Instead, a limiting line can only be developed for uneven-aged, mixed species stands taken as a whole, not for each individual species. Our study confirmed this conclusion.

Kelty (1992) reviewed many studies on yield comparisons of mixedwood versus pure species stands and concluded that the yields of mixedwood stands are generally higher compared to those of pure species stands through competition reduction or growth facilitation. For example, MacPherson et al. (2001) reported a 10% increase in stand total yields (biomass) for mixed aspen and white spruce stands compared to those of pure aspen stands in Alberta. It is speculated that the maximum mean tree size at a given stand density might be larger in mixedwood stands due to the higher potential yields (Binkley 1984). However, most of these studies are not based on similar densities. Instead, densities in mixedwood stands are generally much higher than the pure species stands they were compared to. Compared to pure species stands, differences in tree size can be quite high in mixedwood stands. Therefore, a larger mean tree size (e.g., quadratic mean diameter) in a mixedwood stand is not guaranteed, given the same stand density for both pure and mixedwood stands. This study was aimed at developing a parsimonious relationship to constrain the empirical mortality functions used in MGM. Therefore, no attempt was made to examine productivity differences in pure species stands and various mixtures of different species.

## References

Alberta Land and Forest Service, 1998. Land and forest service permanent sample plot field procedure manual. Alberta Land and Forest Service, Edmonton, Alberta, 110 p.





- Bazzaz, F. A., and Haper, J.L., 1976. Relationship between plant weight and numbers in mixed populations of *Sinapsis alba* (L.) Rabenh. and *Lepidium sativum* L.. J. appl. Ecol., 13 (1), 211-216.
- Binkley, D., 1984. Importance of size-density relationships in mixed stands of Douglas-fir and red alder. For. Ecol. Manage., 9, 81-85.
- Borders, B.E., 1989. Systems of equations in forest stand modeling. For. Sci., 35, 548-556.
- Burkhart, H.E., and Sprinz, P.T., 1984. Compatible cubic volume and basal area projection equations for thinned old-field loblolly pine plantations. For. Sci., 30, 86-93.
- Clutter, J.L., 1963. Compatible growth and yield models for loblolly pine. For. Sci., 9, 354-371.
- Daniels, R.F., and Burkhart, H.E., 1988. An integrated system of forest stand models. For. Ecol. Manage., 23, 159-177.
- Drew, T.H., and Flewelling, J.W., 1977. Some recent Japanese theories of yield density relationships and their application to Monetary pine plantations. For. Sci., 23, 517-534.
- Drew, T.H., and Flewelling, J.W., 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci., 25, 518-532.
- Flewelling, J.W., and Pienaar, L.V., 1981. Multiplicative regression with lognormal errors. For. Sci. 27, 281-289.
- Gertner, G., 1987. Approximating precision in simulation projections: an efficient alternative to Monte Carlo methods. For. Sci., 33 (1), 230-239.
- Huang, S., 1992. Diameter and height growth models. Ph.D. thesis, University of Alberta, Canada, 202 p.
- Huang, S., 1997. A subregion-based compatible height and site index model for young and mature white spruce in Alberta. For. Manage. Res. Note, No. 7, Pub. No., T/354. Alberta Land and Forest Service, Edmonton, Alberta, 32 p.
- Huang, S., Titus, S.J., and Klappstein, G., 1997a. A compatible height and site index model for young and mature aspen based on natural subregions. For. Manage. Res. Note, No. 8, Pub. No., T/355. Alberta Land and Forest Service, Edmonton, Alberta, 28 p.
- Huang, S., Titus, S.J., and Morgan, D., 1997b. Subregion-based compatible height and site index models for young and mature stands in Alberta: revisions and summaries (Part I). For. Manage. Res. Note, No. 9, Pub. No., T/389. Alberta Land and Forest Service, Edmonton, Alberta, 60 p.
- Huang, S., Titus, S.J., Price, D., and Morgan, D., 1999. Validation of ecoregion-based taper equations for white spruce in Alberta. The Forestry Chronicle, 75 (2), 281-292.



- Hynynen, J., 1993. Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. Scan. J. For. Res., 8 (3), 326-336.
- Jack, S.B., and Long, J.N., 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. For. Ecol. Manage., 86, 205-220.
- Kelty, M.J., 1992. Comparative productivity of monocultures and mixed species stands. In: M.J. Kelty, B.C. Larson, and C.D. Oliver (eds). The ecology and silviculture of mixed-species forests. pp. 125-141. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- LeMay, V.M., 1990. MSLS: a linear least squares technique for fitting a simultaneous system of equations with a generalized error structure. Can. J. For. Res., 20 (12), 1830-1839.
- Lloyd, F.T., and Harms, W.R., 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Annals of botany, 57 (5), 681-688.
- Lynch, T.B., and Murphy, P.A., 1995. A compatible height prediction and projection system for individual trees in natural even-aged shortleaf pine stands. For. Sci., 41, 194-209.
- MacPherson, D.N., Lieffers, V.J., and Blenis, P.V., 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For. Chron., 77 (2), 351-356.
- Malmberg, C., and Smith, H., 1982. Relationship between plant weight and density in mixed populations of *Medicago sativa* and *Trifolium pratense*. Oikos., 38, 365-368.
- McCarter, J.B., and Long, J.N., 1986. A lodgepole pine density management diagram. West. J. Appl. For., 1, 6-11.
- McTague, J.P., and Bailey, R.L., 1987. Compatible basal area and diameter distribution models for thinned loblolly pine plantations in Santa Catarina, Brazil. For. Sci., 33, 43-51.
- Miller, D.M., 1984. Reducing transformation bias in curve fitting. The American Statistician, 38, 124-126.
- Mitchell, K.J., 1975. Dynamics and simulated yield of Douglas-fir. For. Sci. Monog. 17, 39 p.
- Neter, J., Wasserman, W., Ketner, M., 1990. Applied linear statistical models. 3rd edn, Irwin, Inc., US, 1181 p.
- Puettmann, K.J., Hann, D.W., and Hibbs, D.E., 1993. Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. For. Sci., 39 (1), 7-27.
- Ratkowsky, D.A., 1990. Handbook of nonlinear regression models. Marcel Dekker, Inc., New York, 241 p.



- Reineke, L.H., 1933. Perfecting a stand density index for even-aged stands. *J. Agric. Res.*, 46, 627-638.
- SAS Institute Inc., 1989. SAS/STAT User's guide. Version 6, fourth edn, Cary, NC, 846 p.
- SAS Institute Inc., 1985. SAS User's guide: Basics, Version 5, Cary, NC, 1290 p.
- Smith, D.J., and Woods, M.E., 1997. Red pine and white pine density management diagrams for Ontario. SCSS technical report. No. 48.
- Solomon, D.S., and Zhang, L., 1998. Maximum size-density relationships for mixed-hardwood forest stands in New England. *In*: M. Hansen and T. Burk (eds). Integrated tools for natural resources inventories in the 21<sup>st</sup> century. pp. 570-579. USDA For. Serv. Gen. Tech. Rep. NC-212.
- Stage, A.R., and Renner, D.L., 1988. Comparison of yield-forecasting techniques using long-term stand histories. *In*: A.R. Ek, S.R. Shifley, and T.E. Burk (eds), Forest growth and yield modeling and prediction. pp. 810-817. USDA For. Serv., Gen. Tech. Rep. NC-120.
- Steel, R.G.D., Torrie, J.H., and Dickey, D.A., 1997. Principles and procedures of statistics: a biometrical approach. 3<sup>rd</sup> edn., The MacGraw-Hill, New York, 666 p.
- Sturtevant, B.R., Bissonette, J.A., and Long, J.N., 1998. Stand density management diagram for mixed balsam fir - black spruce stands. *North. J. Appl. For.*, 15 (1), 17-22.
- Tadaki, T., and Shidei, T., 1959. Studies on the competition of forest trees. II. The thinning experiment on small model stand of Sugi (*Cryptomeria japonica*) seedlings. *Nippon Rin Gakkaishi.*, 41, 341-349.
- Vancly, J.K., 1994. Modeling forest growth and yield: applications to mixed tropical forests. CAB International, UK, 312 p.
- Wang, Y., Titus, S.J., and LeMay, V.M., 1998. Relationships between tree slenderness coefficients and tree or stand characteristics for major species in boreal mixedwood forests. *Can. J. For. Res.*, 28, 1171-1183.
- Westoby, M., 1984. The self-thinning rule. *Advances in Ecol. Res.*, 14, 167-225.
- Wetherill, G.B., Duncombe, P., Kenward, M., Kollerstrom, J., Paul, S.R., and Vowden, B.J., 1986. Regression analysis with applications. Chapman & Hall Ltd., London, 311 p.
- White, J., 1980. Demographic factors in populations of plants. *In*: O.T. Solbrig (eds). Demography and evolution in plant populations. pp. 21-48. Blackwell, Oxford.
- White, J., and Harper, J.L., 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.*, 58, 467-485.





- Wilson, D.S., Seymour, R.S., and Maguire, D.A., 1999. Density management diagram for northern red spruce and balsam fir forests. *North. J. Appl. For.*, 16 (1), 48-56.
- Yao, X., 1997. Modeling juvenile growth and mortality in mixedwood stands of Alberta. Ph.D. thesis. University of Alberta, Edmonton, Alberta, 193 p.
- Yoda, K., Kira, T., Ogawa, H., and Hozumi, K., 1963. Self thinning in overcrowded pure stand under cultivated and natural conditions. *Journal of Biology*. Osaka City University, 14, 107-129.
- Zeide, B., 1987. Analysis of the  $3/2$  power law of self-thinning. *For. Sci.*, 33 (2), 517-537.
- Zhang, S., Amateis, R.L., and Burkhart, H.E., 1997. Constraining individual tree diameter increment and survival models for loblolly pine plantations. *For. Sci.*, 43 (3), 414-423.



Table 3.1. Summary statistics of the permanent sample plot data.

Species	N	mean	min.	max.	std
Basal area (m <sup>2</sup> /ha)					
AW	2809	11.8	0	55.9	10.4
SW	3990	14.3	0	69.3	14.0
PL	3707	23.7	0	64.7	15.3
ALL	5678	38.0	0	87.9	10.8
Density (stems/ha)					
AW	2809	380	5	7615	666.5
SW	3990	507	4	7209	665.3
PL	3707	1264	4	18366	1540
ALL	5678	2019	4	18366	1783
Quadratic mean diameter (cm)					
AW	2809	25.6	1.2	56.6	9.6
SW	3990	19.3	1.2	59.3	9.7
PL	3707	20.9	1.7	51.1	7.9
ALL	5678	18.5	1.7	46.3	6.5
Species composition					
AW	2809	0.3269	0	1	0.2839
SW	3990	0.3556	0	1	0.3172
PL	3707	0.6177	0	1	0.3674
Site index (m)					
AW	141	18.9	12.9	26.0	2.9
SW	358	16.4	6.3	26.6	3.4
PL	288	17.1	4.1	27.1	3.8

Note: AW, SW, and PL represent only trembling aspen trees, white spruce trees, and lodgepole pine trees in any stands and ALL represents all trees in any stands; N is total number of observations (repeated measurements of plots); and mean, min., max., and std are mean, minimum, maximum, and standard deviation, respectively.



Table 3.2. Potential functions for the average QMD-DEN relationship.

Function	Function form
(1)	$QMD = a \cdot DEN^b$
(2)	$QMD = 1/(a+b \cdot DEN)$
(3)	$QMD = a + b \cdot \ln(DEN + c)$
(4)	$QMD = 1/(a + b \cdot DEN^c)$
(5)	$QMD = a \cdot \exp(b/(DEN + c))$

Note: QMD is quadratic mean diameter (cm); DEN is stand density (stems/ha); and a, b, c are the parameters to be estimated.

Table 3.3. Estimated coefficients and MSE for each function in Table 3.2.

Function	a	b	c	n	MSE
(1)	575.6546	-0.4544		339	3.2754
(2)	0.022079	0.00001338		339	1.2664
(3)	82.7550	-8.3127	-113.0316	339	1.6138
(4)	0.01823055	0.00006188	0.82332331	339	0.8713 <sup>1</sup>
(5)	3.64784	10046.31571	3929.22091	339	1.0123 <sup>2</sup>

Note: MSE stands for mean squared error and the two smallest MSEs are ranked as <sup>1</sup> and <sup>2</sup> for model (4) and (5).



Table 3.4. Prediction statistics based on the validation data set (n=129).

Model	$\bar{e}$	$\bar{e} \%$	MSEP	RE%	R <sup>2</sup>
(1)	-0.419	-2.97	3.868	13.94	0.9488
(2)	0.333	2.36	1.202	7.77	0.9851
(3)	0.112	0.79	1.740	9.35	0.9761
(4)	0.062	0.44	0.795	6.32	0.9890
(5)	0.057	0.40	0.870	6.61	0.9881

Note:  $\bar{e}$  is mean prediction bias;  $\bar{e} \%$  is percent bias; MSEP is mean squared error of prediction; RE% is relative error in prediction; and R<sup>2</sup> is coefficient of determination.

Table 3.5. The linear fit between density and quadratic mean diameter in log-log scale.

Species	N	Intercept	Slope	R <sup>2</sup>
AW	933	8.8945	-0.5926	0.2447
SW	1186	8.5152	-0.4812	0.2265
PL	1108	11.046	-1.2083	0.4442
ALL	3227	12.130	-1.6869	0.7395

Note: AW, SW, PL and ALL represent trembling aspen, white spruce, lodgepole pine and all species combined; N is total number of observations.





Table 3.6. Coefficients and MSE for each site productivity class using model (4):  
 $QMD = 1/(a + b \cdot DEN^c)$ .

Site class	a	b	c	n	MSE
Poor	0.0178	0.000080	0.7929	169	0.7438
Medium	0.0187	0.000058	0.8292	130	0.8660
Good	0.0185	0.000051	0.8491	143	0.7289

Note: QMD is quadratic mean diameter (cm), DEN is stand density (stems/ha),  
and MSE stands for mean squared error.



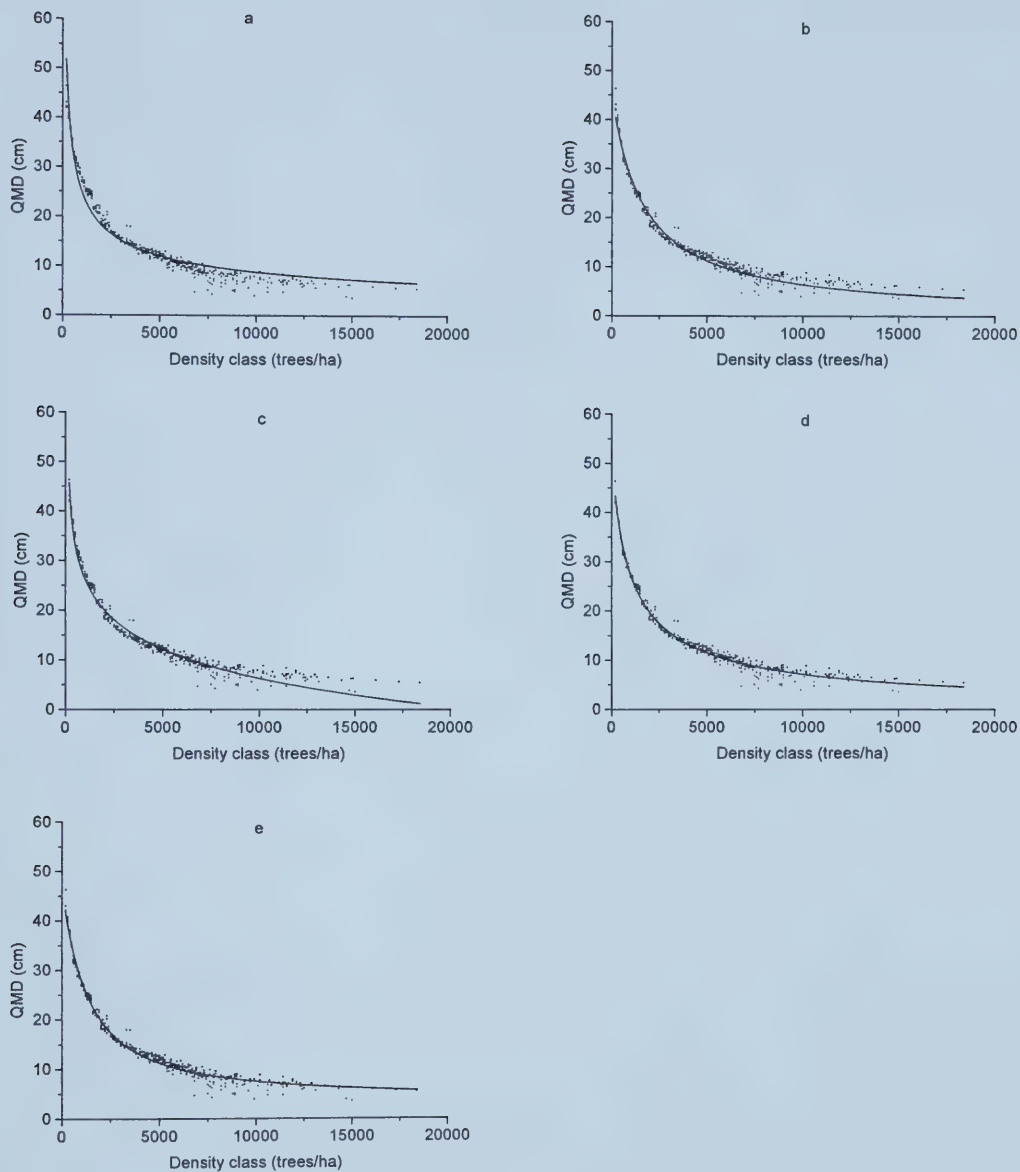


Figure 3.1. Fitted models overlaid with model fitting data ( $n = 339$ . a, b, c, d, e represent model (1), (2), (3), (4), (5)).



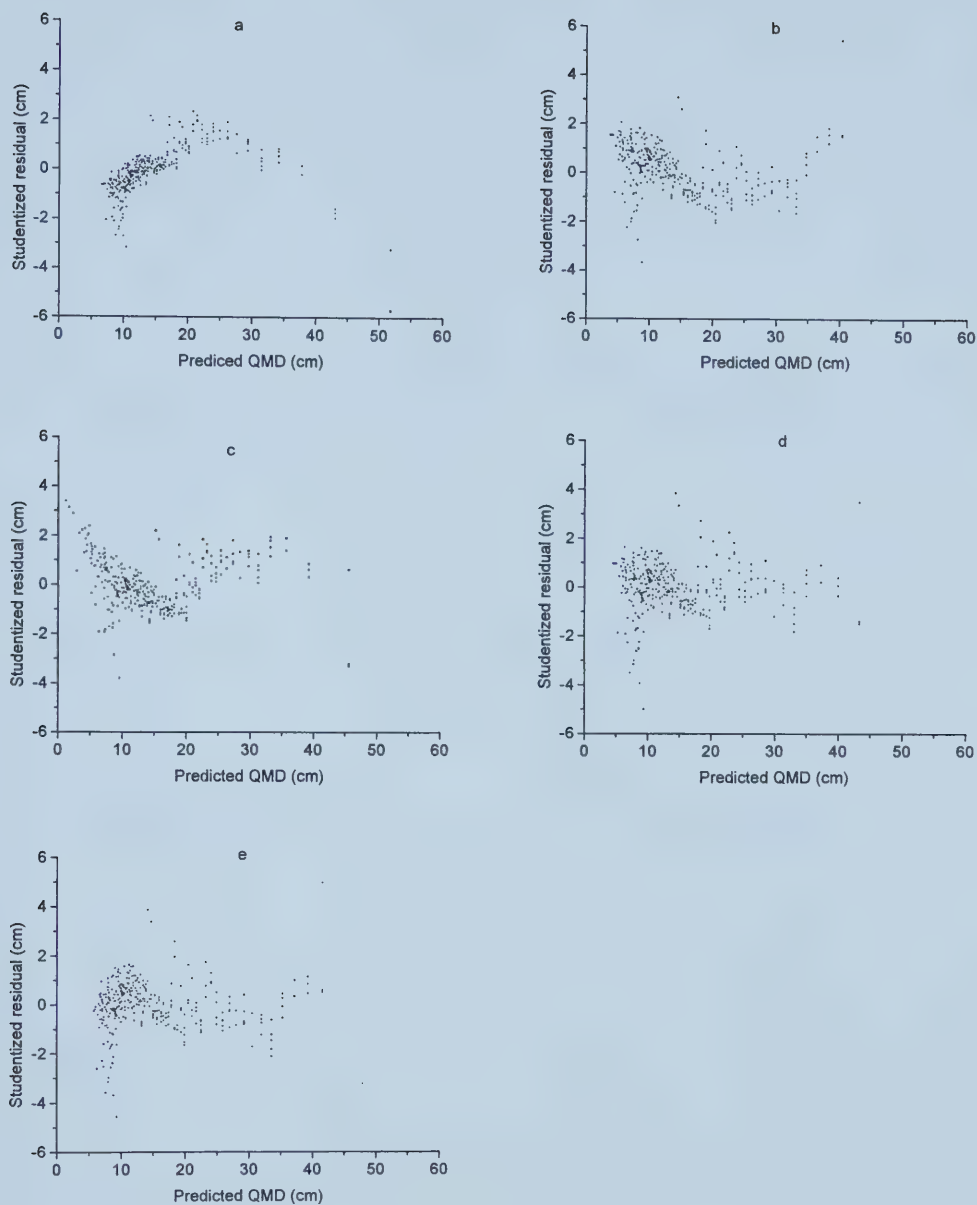


Figure 3.2. Plots of studentized residuals against predicted quadratic mean diameters based on model fitting data (a, b, c, d, e represent model (1), (2), (3), (4), (5)).





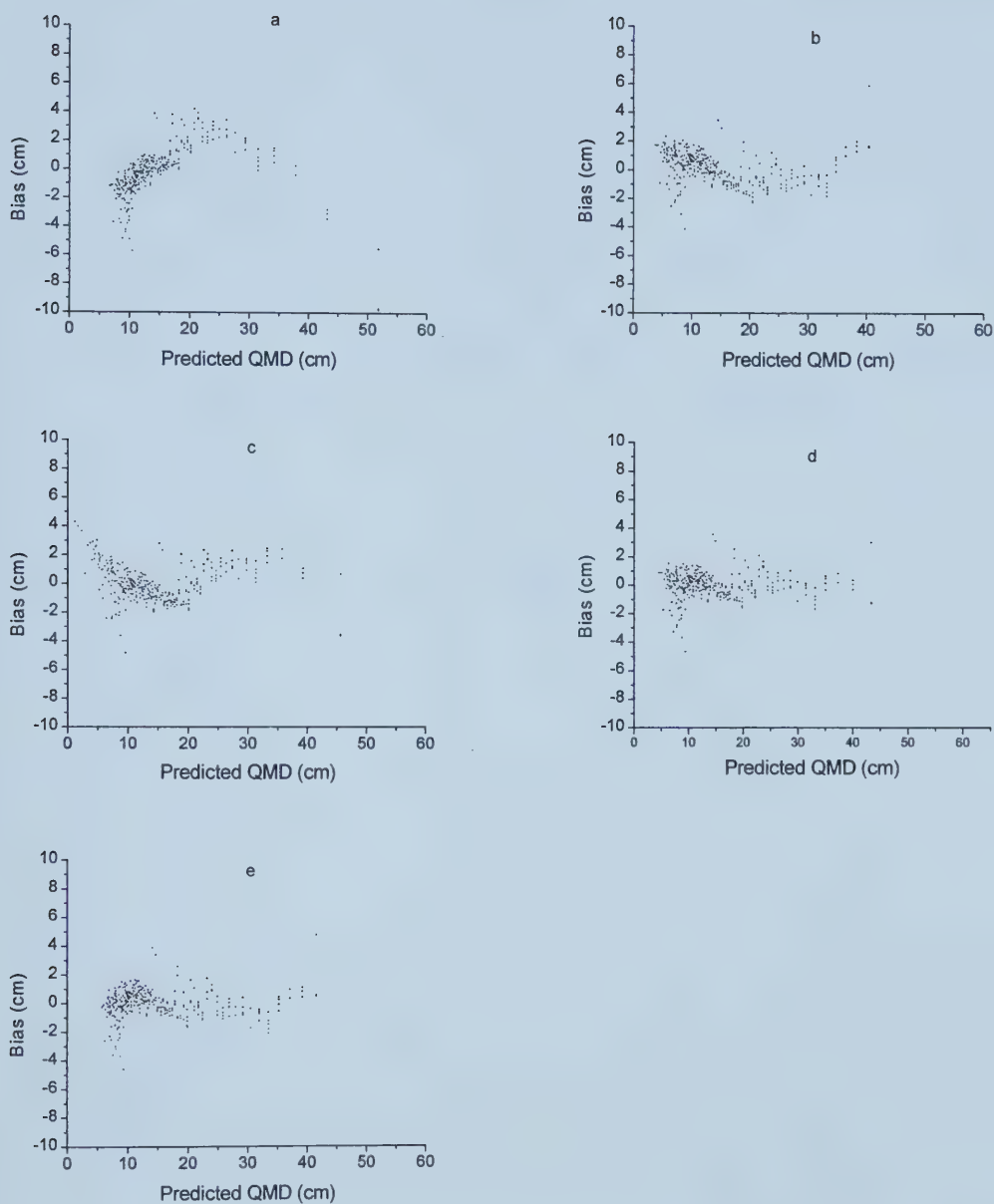


Figure 3.3. Plots of prediction biases against predicted quadratic mean diameters (a, b, c, d, e represent model (1), (2), (3), (4), (5)).



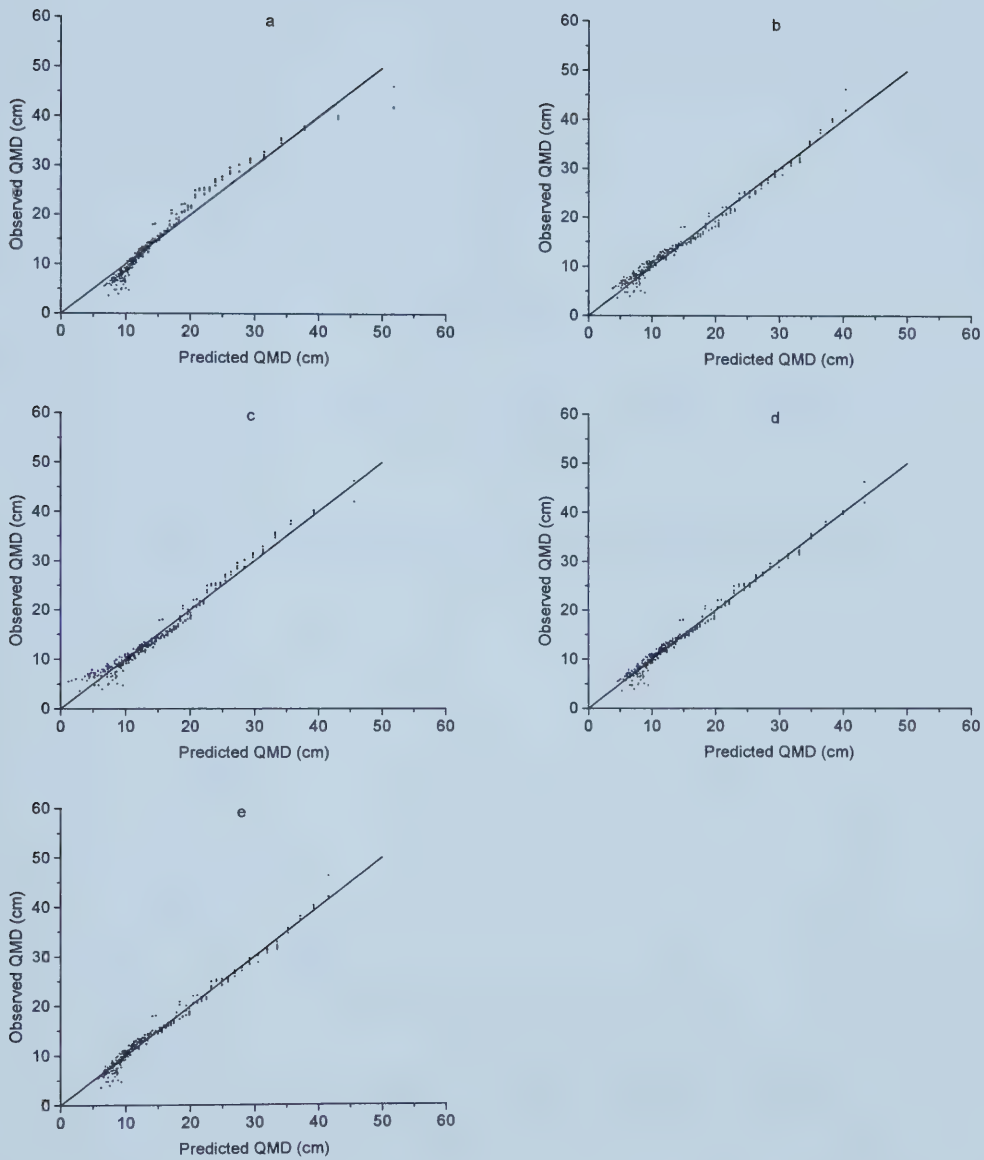


Figure 3.4. Plots of observed against predicted quadratic mean diameters. The diagonal lines indicate that the predicted and observed quadratic mean diameters are equal (a, b, c, d, e represent model (1), (2), (3), (4), (5)).



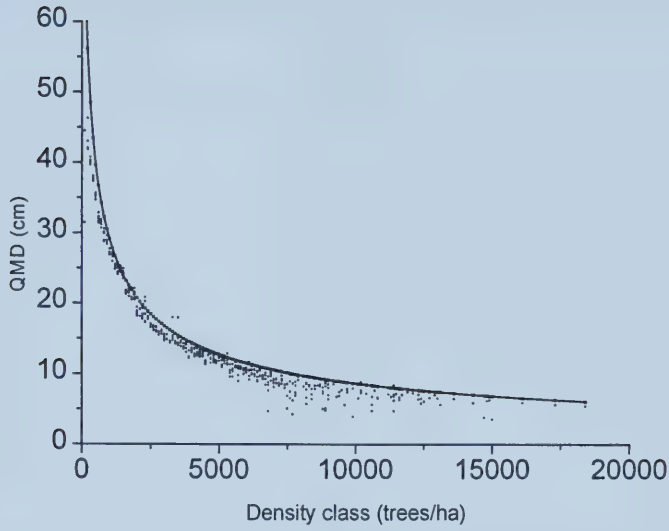


Figure 3.5. The maximum size-density relationship based on model (4).

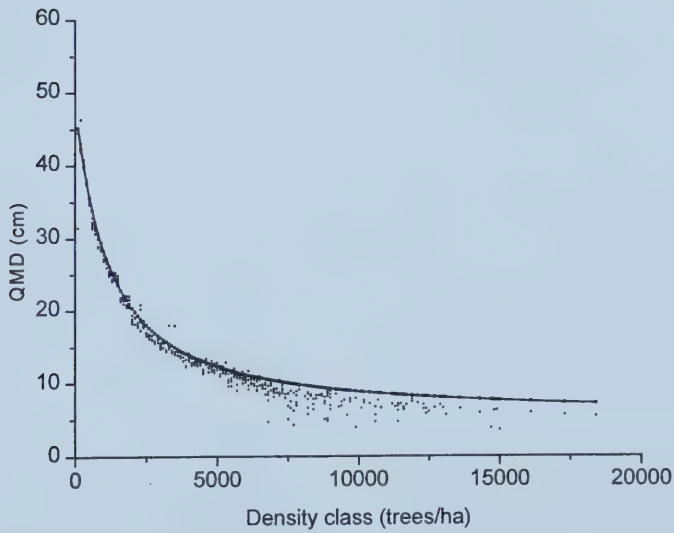


Figure 3.6. The maximum size-density relationship based on model (5).



## Chapter 4. Constraining factors on empirical mortality functions

### 4.1. Introduction

Empirical growth models represent the best fit for the data used for developing these models. They may not behave well when extrapolated beyond the range of the data they were based upon and can lead to unreasonable predictions. In growth modeling, we often have limited, if any, data at extreme stand conditions. These stands might be relatively rare, or they might only occur within a short period of stand development or over a smaller area. For example, it is very easy for aspen and lodgepole pine to regenerate into very dense stands in Alberta. But they only stay very dense for a short period of time (i.e., before the self-thinning phase). Therefore, they are not easily captured through the commonly used sampling procedures. However, it is very important to understand the growth and density changes of stands at this stage because they will ultimately determine the growth and survival of trees in the later stages of stand development. Unless we purposely select and measure those stands, there are often not enough data to represent such stand conditions. Therefore, empirical growth models are often extrapolated beyond the data ranged used for their developments.

To ensure reasonable model performances when extrapolated, theoretical constraints can be used to expand the usage of a growth model. However, it is always difficult to constrain a growth model and have it perform well when extrapolated. Ecological theories relating to processes for extreme stand conditions are often incomplete and make the constraints somewhat uncertain. Still, they are preferred to relying on the empirical fits alone (Cao 1994).

This study was under the framework of The Mixedwood Growth Model (MGM) developed at the University of Alberta. "MGM is a deterministic, distance-independent, individual tree based stand growth model that is capable of summarizing both tree and stand characteristics for major boreal mixedwood species" (<http://www.rr.ualberta.ca/research/mgm/mgm.htm>). The empirical mortality functions developed in Chapter 2 for trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus*





*contorta* Dougl. ex Loud. var. *latifolia* Engelm) were incorporated into MGM. Various MGM simulations revealed several problems.

One major problem was that the projected stand volumes increased continuously with increasing stand initial densities. This resulted in excessive yields for stands with excessive starting densities, which is not realistic.

Theoretically, starting from a very low density, the maximum attainable stand yield increases with increasing initial density, but only to a point. This point is where a stand is fully stocked. Beyond this point, further increase in initial density will not result in any further increase in the maximum achievable stand volume (Craig Farnden, forestry consultant, Prince George, personal communication).

Closer examination of MGM outputs revealed that high volumes associated with dense stands were caused by the empirical mortality functions. Mortality rates were not high enough in these dense stands. However, individual trees still grew at higher rates as if stand densities were not that high. This was contradictory to the well-accepted self-thinning theory. According to the self-thinning theory, there is an upper limit between stand density and average tree size. A stand can occupy any point below the limit, but not above the limit. At the limit, larger trees will continue to grow larger at the expense of smaller ones (Yoda et al. 1963, Drew and Flewelling 1977, Peet and Christensen 1987, Zeide 1991, Hynynen 1993). Therefore, in very dense stands, tree mortality rates should be quite high to maintain the stands below the self-thinning line (the limit).

Although the maximum size-density relationship developed in Chapter 3 was effective in constraining the empirical survival functions in most situations, it did not help in reducing stand densities to a reasonable level for very dense stands. The same data (Alberta PSP data) were used to develop that relationship and there were no data on very dense stands. In fact, almost all stands in the PSP data set were less than 15,000 stems/ha with only a few stands between 15,000 stems/ha and 18,000 stems/ha. When applied beyond the density of 18,000 stems/ha, this relationship is also extrapolated and becomes less reliable.



Another problem was with old stands of aspen and lodgepole pine. These two species are short-lived stands and are expected to break up as the trees approach old age. However, MGM simulations showed that even at very old ages, stands of aspen and lodgepole pine were still growing strong without any sign of stand breakup.

The objective of this study was to develop a set of theoretical constraining factors and impose them on the empirical mortality functions developed for aspen, white spruce, and lodgepole pine. These factors will be used to overcome the problems discussed above.

#### **4.2. The data**

The Permanent Sample Plot (PSP) data, collected by Alberta Land and Forest Service over the past 40 years throughout the forested area in the province of Alberta, were used in this study. The data were from 699 locations and covered wide ranges of ages, stand densities, species compositions, and site conditions. At each of the 352 locations there was a cluster of 4 plots, while there was only one plot at each of the remaining 347 locations. Detailed information can be found in the permanent sample plot field procedure manual (Alberta Land and Forest Service 1998). There were 1755 plots in total with up to six remeasurements of individual tree characteristics. All the data were used for this study.

#### **4.3. Methods**

##### **4.3.1. Constraints for dense stands**

As discussed in the introduction, projected stand volumes were very high for stands with high initial densities. An example of this extrapolation problem is illustrated in Fig. 4.1 using pure aspen stands, where a, b, and c are for good sites (site index 22 m), medium sites (site index 18 m), and poor sites (site index 14 m), respectively. Stands with various initial densities, ranging from 600 stems/ha to 70,000 stems/ha, are projected for 240 years. Starting from the initial density of 600 stems/ha, projected stand volume increases with increasing initial density. On good sites, projected volumes peak around 900 m<sup>3</sup>/ha for a stand with initial density of 70,000 stems/ha. Similar results are found for aspen stands on the other two sites (see Fig. 4.1) and for the other two species (graphs not shown). For white spruce, the peak volume of the same density stand on good sites (site index 22m) is more than 850 m<sup>3</sup>/ha and it is more than 1000 m<sup>3</sup>/ha for lodgepole pine. On less productive sites, these volumes are a bit lower, but still unrealistically high.



Lack of data on dense stands lead to the extrapolation of the developed empirical mortality functions when applied to these stands, which results in excessive volumes. Table 4.1 presents stand density percentiles for pure aspen stands, pure white spruce stands, pure lodgepole pine stands, and all stands combined. A stand is considered to be a pure species stand if the target species composition is equal to or greater than 80% by basal area (Burns and Honkala 1990, Huang 1992). Species composition is calculated as the ratio of the target species basal area to stand total basal area. It is clearly shown in Table 4.1 that no aspen density is above 8000 stems/ha and most of them (95%) are below 5000 stems/ha. Corresponding density limits for pure white spruce stands are even lower. Almost all white spruce stands (99%) are below 5000 stems/ha. For pure lodgepole pine stands, there are a few stands with larger densities, but only to about 10,000 stems/ha with the majority of them (95%) below 6000 stems/ha. When all stands are pooled together, the majority of stands (99%) are below 8000 stems/ha. Therefore, it is not surprising that the developed mortality functions do not perform well when extrapolated to very dense stands.

A similar problem was also reported in another growth model Prognosis (Wykoff et al. 1982). Prognosis is also an individual tree based growth model that is widely used in US and parts of Canada (British Columbia) with about 20 regional variants. Due to the empirical nature of this model, various constraining factors (multipliers) for different model components have been developed and are a common feature of most versions of Prognosis (Hamilton 1994).

One specific problem with the empirical mortality function in Prognosis was that in dense stands where accelerated mortality was expected due to competition, the predicted tree mortality rates were too low. A constraining factor based on the defined maximum stand basal areas was imposed on the empirical mortality model to increase tree mortality rates. According to Wykoff et al. (1982), there is a maximum potential a site can support and this potential can be represented by stand basal area. Sterba and Monserud (1993) adopted this method to develop a maximum size-density relationship for uneven-aged multi-species stands by applying directly the maximum basal areas defined by Wykoff et al. (1982).

A stand with very low density normally does not fully occupy the site. The occupancy of the site increases with increasing stand density, which leads to increased stand volume. Once the





maximum potential of a site is reached, further increases in stand density will not result in further increases in stand volume. Craig Farnden (forestry consultant, Prince George, personal communication) suggested that the lower density range of this maximum potential was in the range of 1000 to 2000 stems/ha for conifers species in the interior of British Columbia, and is similar for aspen. We assume that common species in Alberta also fall in this density range, beyond which there is little variation in the maximum achievable stand volumes.

The maximum basal area idea was used in this study to develop a set of constraining factors for the empirical mortality functions. These factors were developed to prevent unrealistic volumes for very dense stands. Stand basal area is considered a better measure of stand occupancy since site occupancy is a combination of tree size and tree numbers. Based on Alberta permanent sample plot data, one maximum stand basal area ( $BA_{SPmax}$ ) was defined respectively for pure aspen stands, pure white spruce stands, pure lodgepole stands, and mixedwood stands. Basal area percentiles and the summary of stand basal areas by diameter and density classes were used to define the maximum stand basal areas. The guideline was to have the majority of stand basal areas below the defined maximum basal areas.

With the defined maximum stand basal areas and stand projected basal areas, a constraining factor was formulated:

$$F_1 = \begin{cases} 1 - \frac{BA - BA_{SPmax}}{m} & (\text{if } BA > BA_{SPmax}) \\ 1 & (\text{if } BA \leq BA_{SPmax}) \end{cases} \quad (1)$$

where BA is projected stand basal area from MGM,  $BA_{SPmax}$  is the defined maximum stand basal area by species, and m is a constant.

This constraining factor was designed to be between zero and one by using a large constant m. It was a simple function of the defined maximum basal area and the projected stand basal area. As growth projection continues, if the projected stand basal area of a stand is larger than the defined maximum basal area, this factor will be activated. Factor  $F_1$  decreases as the difference between the projected and the maximum basal areas increases. If the projected stand basal area is only slightly larger than the maximum basal area, factor  $F_1$  should be close to one. This was achieved by a large constant m. Stand volumes from Alberta Normal Yield Tables and the upper bound of stand volumes from the provincial PSP data were used to guide the final selection of the constant m.



Table 4.2 lists stand volumes of aspen, white spruce, and lodgepole pine at 100 and 150 years on three sites from Alberta Normal Yield Tables (Alberta Energy and Natural Resources 1985). At 100 years, total volumes for aspen stands (utilization standard 0/0) reach 362.4 m<sup>3</sup>/ha on good sites, 268.17 m<sup>3</sup>/ha on medium sites, and 182.23 m<sup>3</sup>/ha on poor sites. At 150 years, these volumes are 431.2 m<sup>3</sup>/ha, 327.66 m<sup>3</sup>/ha, and 228.68 m<sup>3</sup>/ha for the three site classes. Similar volumes can be read from the table for the other two species. These volumes are used as proxies of maximum allowable stand volumes and subsequently used for the selection of the constant value  $m$  in the factor  $F_1$  to achieve proper reduction on individual tree survival rates because the ultimate goal is to reduce the unreasonably high stand volumes for very dense stands.

In addition, stand volumes from the PSP data were summarized to search for an upper bound for each species. The percentiles for stand volumes are shown in Table 4.3 for pure stands of aspen, white spruce, and lodgepole pine, and for mixedwood stands (all species combined). Since the objective is to find the maximum attainable volumes for each species, only percentiles of 75% and up are presented. These volume percentiles and stand volumes from Alberta Normal Yield Tables are used together to determine the constant  $m$  in equation (1). The guiding principle is to have reasonable volume projections for any density stand.

The constraining factor  $F_1$  will be used to reduce the survival rates of individual trees in dense stands by multiplying it by the predicted survival probability ( $P_s$ ) of an individual tree:

$$P_{s_1} = P_s * F_1 \quad (2)$$

Equation (2) will be activated once the projected stand basal area is above the maximum basal area. The bigger the projected stand basal area is compared to the maximum basal area, the smaller the constraining factor  $F_1$  is, and the more reduction on the survival rates of individual trees.

#### **4.3.2. Constraints for very large trees**

In young stands, larger trees are usually more competitive than smaller trees in accessing limited resources. Therefore, they are more vigorous and are expected to have higher survival rates compared to less vigorous smaller trees in the absence of unusual mortality agents (e.g.,



insect infestation). As stands approach maturity, however, larger trees are at competitive disadvantage in terms of growth and survival. Several factors are responsible for the decline in the growth and survival of large trees.

First, respiration increases with tree size. Maximum photosynthetic surface area (canopy leaf areas) is reached quite early in stand development and stabilize or decline afterwards. Non-photosynthetic tissues, however, continue to increase with increasing tree size. Therefore, the ratio of non-photosynthetic tissues to photosynthetic tissues is bigger for larger trees. Subsequently, there is less photosynthate available for tree growth (Waring and Schlesinger 1985, Waring 1987, Barnes et al. 1998).

In addition, Long and Smith (1992) revealed that instead of stabilizing after crown closure, stand leaf area index tends to decrease. The reduction in growth rates of larger trees is not only a result of increased respiration, but also a result of declined leaf area index. The declining leaf area index is associated with crown shyness (Long and Smith 1992). As stand average height increases, trees tend to be more slender and crown margins are abraded as adjacent trees sway in the wind. This prunes and reshapes the crowns so that they become narrower and more elongated.

Also, there is evidence that whole tree hydraulic conductivity declines with tree age and size (Köstner et al. 1996, Ryan and Yoder 1997), possibly due to increased length of pathway for water to travel, reduced xylem conductivity in roots, branches, and stems, and changes in sapwood permeability (Hubbard 1999). Reduced hydraulic conductivity of old trees will limit their photosynthesis by stomatal closure due to increased water stress in leaves (Ryan and Yoder 1997, Hubbard et al. 1999).

As a result, growth rates of large trees decrease sharply and they become more vulnerable to disease, wind, and other mortality agents with increased mortality rates.

Wykoff et al. (1982) defined a stand as an old stand if its quadratic mean diameter is above a threshold quadratic mean diameter. A new variable  $Z$  was calculated for an old stand based on projected stand quadratic mean diameter and the defined quadratic mean diameter limit:





$$Z = \frac{(\text{QMD}_{\text{SP}} - \text{QMD}_{\text{SPlimit}})^2}{C} \quad (3)$$

where  $\text{QMD}_{\text{SP}}$  is projected quadratic mean diameter (cm) and  $\text{QMD}_{\text{SPlimit}}$  is the defined threshold of stand quadratic mean diameter (cm) by species beyond which a stand is considered as an old stand.

In an old stand, if the diameter of an individual tree is bigger than the quadratic mean diameter of that stand, this tree is defined as an old tree and should receive a reduction on its survival rate regulated by a constraining factor. This factor is a function of the variable  $Z$  from equation (3), quadratic mean diameter of the stand ( $\text{QMD}_{\text{SP}}$ ), and the diameter (DBH) of that tree (Wykoff et al. 1982):

$$F_2 = \begin{cases} \frac{1 + Z * (\text{QMD}_{\text{SP}} / \text{DBH})}{1 + Z} & \text{(if } \text{QMD}_{\text{SP}} > \text{QMD}_{\text{SPlimit}} \text{ and } \text{DBH} > \text{QMD}_{\text{SP}}) \\ 1 & \text{otherwise} \end{cases} \quad (4)$$

A similar method was used in this study to reduce the survival rates of old trees in old stands. Instead of selecting an arbitrary quadratic mean diameter as the threshold as in the Prognosis model, the upper boundary of quadratic mean diameters from PSP data were used to define the threshold value beyond which a stand is considered as an old stand. For each species, the quadratic mean diameters of all pure species stands were used for this purpose. A stand is considered as a pure species stand if the composition of one species is greater or equal to 80% by basal area. A quadratic mean diameter limit was defined for each species based on the percentiles of the quadratic mean diameters. A value close to the 90<sup>th</sup> percentile was chosen to approximate the quadratic mean diameter threshold beyond which a stand was defined as an old stand.

The same formulation (equations (3) and (4)) was used in this study. When the difference between projected the quadratic mean diameter and the threshold limit is small, the factor  $F_2$  should be close to 1 so that the reductions on the survival rates of large trees are very small. A large constant denominator  $C$  was selected to ensure that the value of  $Z$  is close to 0 and consequently, the factor  $F_2$  is close to 1. In equation (3), the difference between the projected and the threshold quadratic mean diameters was squared to increase the value of  $Z$  when the





projected quadratic mean diameter is much larger than the threshold quadratic mean diameter. This will increase the effect of the ratio variable ( $QMD_{sp}/DBH$ ) in equation (4).

With the defined quadratic mean diameter threshold for each species, the constraining factor given by equation (4) was multiplied by the predicted survival probability ( $P_s$ ) of an individual tree from the empirical mortality function:

$$Ps_2 = Ps * F_2 \quad (5)$$

Equation (5) will only operate in MGM when the following two conditions are met:

- the projected quadratic mean diameter of a stand is above the defined quadratic mean diameter threshold; and
- the diameter of an individual tree is larger than the projected quadratic mean diameter.

When factor  $F_2$  is activated, the ratio of quadratic mean diameter to individual tree diameter ( $QMD_{sp}/DBH$ ) is always less than 1, so does the constraining factor  $F_2$  based on the formulation of factor  $F_2$ .

#### 4.3.3. Constraints for old stand breakup

For relatively long-lived species like white spruce, the constraining factor  $F_2$  based on the quadratic mean diameter limit is sufficient to reduce the survival rates of large old trees. However, for short-lived aspen and lodgepole pine, stands are expected to break up eventually at old ages. An example for aspen stands is illustrated in Fig. 4.1. Even at 240 years, the projected stand volumes of various initial stand densities are still quite high on all three sites. Both species are expected to die out somewhere between 100 and 200 years, depending on many factors such as site conditions, forest fires, and insect and disease breaks. Aside from their short-lived nature, frequent fires will prevent them from getting really old.

Aspen is a fast growing and short-lived tree species. However, aspen stand breakup is not yet well understood in the boreal region of the Prairie Provinces (Peterson and Peterson 1992). Fralish (1972) suggested that the breakup of natural aspen stands does not occur at the same age throughout its geographic range, but varies with climatic conditions. Burns and Honkala (1990) showed that a few vigorous aspen stands are about 200 years in Alaska and the Rocky Mountain region. In Fort Nelson District of British Columbia, some aspen stands are more



than 150 years but still quite healthy with virtually no stem decay (Craig Farnden, forestry consultant, Prince George, personal communication). Alberta PSP data showed that almost all aspen stands (99%) with age information are less than 130 years old, with the oldest stand being 153 years old.

Although aspen stand breakup happens at different ages, it does tend to follow a certain pattern. The deterioration begins when crowns can no longer grow fast enough to fill the canopy gaps generated by dead trees. Stands at this stage are subjected to increased exposure to wind and evaporation. Aspen is intolerant to these sudden stresses and becomes susceptible to disease and insect attacks due to loss of vigor. Increased breakage accelerates the deterioration process, which may be completed in as few as 3 or 4 years in the eastern US. This process is much slower in the western US (Burns and Honkala 1990).

Life span for lodgepole pine stands is much more variable. In northern Idaho and central Oregon, stands start to break up at about 80 to 100 years, while stands at higher elevations, such as in Montana, southern Idaho, Utah, and Wyoming, last for several hundred years (Burns and Honkala 1990). In interior British Columbia, the summary data derived from a large permanent sample plot data set showed that 95% of lodgepole pine trees were less than 170 years on good and medium sites. It is assumed that stands normally do not live beyond that age. On poor sites, trees may live much longer than 170 years. This includes lodgepole pine trees in both pure lodgepole pine stands and mixedwood stands (Cam Bartram, forester, Ministry of Sustainable Resource Management in Victoria, personal communication). Smither (1961) reported that lodgepole pine stands live up to about 150 years in Alberta. While individual trees may remain sound for much longer, mortality among the largest trees causes the stand to decline rapidly beyond this age. Alberta PSP data showed that 99% of the lodgepole pine stands with age information available were below 150 years old. Separation of these stands by site classes revealed that stands on poor sites were older than those stands on good and medium sites.

To break up old aspen and lodgepole pine stands, another constraining factor was introduced. This factor was based on average height growth rate of the top height trees in a stand. Top height trees were selected using the widely used criterion: 100 largest diameter trees per hectare.



As trees grow from maturity to old age, tree height growth decreases sharply and so does tree volume growth (Waring and Schlesinger 1985, Yoder et al. 1994, Ryan and Yoder 1997). Old trees are different from young trees both physiologically and morphologically. They have lower photosynthesis rates and reduced height and diameter growth rates. Photosynthesis is reduced as a result of reduced hydraulic conductivity. In addition, slow xylem growth will result in small vessels, which will increase hydraulic resistance (Ryan and Yoder 1997). This negative loop suggests that stem growth in old trees should be most severely limited where hydraulic resistance is greatest: at the tops of tall trees or the tips of very long branches (Ryan and Yoder 1997). With less produced photosynthate due to increased hydraulic conductance, trees are less vigorous and are susceptible to diseases and insects at old ages. Mortality rates are therefore very high. When this happens, it won't take long for stands to breakup.

Another reason for using height growth of the top height trees, is that height growth is less affected by stand density. In addition, height growth reflects the average of influences from more than one year and is not affected by weather fluctuations as much as diameter growth is (Oliver and Larson 1996).

Beck (1971) found that in even-aged stands, tree height growth of white pine peaks earlier and declines more rapidly on good sites. Ryan et al. (1997) reported that this is a general trend for most species. Therefore, stands on good sites are expected to die out earlier than those on poor sites. For lodgepole pine, this was supported by both Alberta and British Columbia PSP data discussed earlier. The trend was less obvious for aspen using Alberta PSP data due to inadequate number of stands with both stand age and site index information.

The site index curves developed by Huang et al. (1997a, 1997b) for aspen and lodgepole pine were used to define the height growth limits of the top height trees, below which stands start to break up. These curves were developed using stem analysis data from dominant and codominant trees and were applied here to approximate the height growth rates of the top height trees. Due to the objective selection criterion used (100 largest diameter trees per hectare), top height trees were adopted in this study to develop the stand breakup factor.





For both aspen and lodgepole pine, a reference site index ( $SI_{SPref}$ ) was selected and the height growth rates at various ages based on that site index curves were used to define the threshold values for stand breakup. The average site index values for good sites based on Alberta phase 3 inventory data were used as the reference site index, i.e., site index 20 m for aspen ( $SI_{AWref}$ ) and site index 18 m for lodgepole pine ( $SI_{PLref}$ ) (Alberta Energy and Natural Resources 1985). Based on the available information on stand breakup, it was decided in this study that for aspen stands on good sites with a site index 20 m, the initiation of stand breakup was about 130 years breast height age. Accordingly, the height growth rate at 130 years of breast height age from aspen site index curve was defined as the threshold value. Correspondingly, breast height age of 140 years was chosen to be the initiation age of the breakup of lodgepole pine stands with site index 18 m. Height growth rate at that age from pine site index curve was defined as the height growth limit.

Since height growth is directly affected by site quality, the height growth limit should be a function of site index. Although it is generally reasonable to assume that stands on good sites break up earlier than those on poor sites, no quantitative information is available on the exact effect of site quality on the initiation of stand breakup. For this study, a simple ratio, the ratio of the site index of a particular stand to the reference site index was used to scale the height growth limit of the top height trees. It was multiplied by the height growth limit from the reference site index curve:

$$HTINC_{SPlimit} = HTINC_{SPref} * (SI/SI_{SPref}) \quad (6)$$

where  $HTINC_{SPlimit}$  is the height growth limit of the top height trees of a stand,  $HTINC_{SPref}$  is the height growth limit from the reference site index curve,  $SI$  is stand site index, and  $SI_{ref}$  is the reference site index for the species.

For a particular stand, if the average height growth of the top height trees is below the defined threshold in equation (6), stand deterioration begins. The difference between the average height of the top height trees and the height of each individual tree was used to determine if a particular tree will receive reduction on its survival probability. According to Alberta vegetation inventory standards (Alberta Environment Protection 1991), if the difference between the average height of the canopy layer and the average height of another layer in the understory is above 3 meters, they are considered as two different layers. A similar approach was used in this study to determine if a tree was in the same canopy layer as other old trees to



receive reduction on its survival rate. If the height of an individual tree was within 3 m of the average height of the top height trees, this tree was considered in the same canopy layer as the top height trees and will receive a reduction on its survival rate. Therefore, for a particular stand, once the average height growth of the top height trees is below the specified limit, all trees that are in the same layer as the top height trees receive reductions on their survival rates to break up the stand. Younger trees regenerated later will not contribute to stand breakup and will not have their survival rates modified.

Although it is well accepted that short-lived aspen and lodgepole pine stands will breakup eventually, no quantitative information is available on the speed of stand breakup. As discussed earlier, stand breakup for aspen is quite slow in the western US (Burns and Honkala 1990). The speed of stand breakup for aspen and lodgepole pine in Alberta is also quite slow. It is probably reasonable to assume that stand breakup needs about 20 to 30 years to complete for both species (Grant Klappstein, forester, Alberta Sustainable Resource Development, Edmonton, personal communication).

In this study, a simple factor, a constant number K ranging between zero and one was used as the constraining factor for both species once the height growth of the top height trees ( $HTINC_{sp}$ ) is below the defined height growth limit:

$$F_3 = \begin{cases} K & (\text{if } HTINC_{sp} < HTINC_{limit}) \\ 1 & (\text{if } HTINC_{sp} \geq HTINC_{limit}) \end{cases} \quad (7)$$

$F_3$  was further applied to reduce the survival rates of all the old trees in a stand. It was multiplied by the probability of survival ( $P_s$ ) predicted by the empirical survival function:

$$Ps_3 = F_3 * Ps \quad (8)$$

Various tree survival probabilities at the beginning of stand breakup were multiplied by different K values in the range of 0 and 1. Trees with very small survival rates at the beginning of stand breakup are very likely to die out even without any reduction on their survival rates. To a large extent, the number of years needed for a stand to break up depends on the reduction rates on trees with high survival probabilities at the beginning of stand breakup. A final constant K was selected so that trees with large survival probabilities will die out in about 20 to 30 years. As stand projection continues for an aspen or a lodgepole stand,



once the average height growth rate of the top height trees is below the defined threshold, equation (8) will be activated. The survival rates of individual trees that are in the same canopy layer as the top height trees are reduced to achieve stand breakup.

## 4.4. Results

### 4.4.1. Constraints for dense stands

Table 4.4 presents the percentiles (50% and above) for stand basal areas for pure aspen, pure white spruce, pure lodgepole pine, and all species combined.

For pure aspen stands, the 90<sup>th</sup> percentile of stand basal area is slightly larger than 40 m<sup>2</sup>/ha. Table 4.5 gives the averaged aspen basal areas by quadratic mean diameter and density classes. It is clearly shown that large basal areas (those bigger than 40 m<sup>2</sup>/ha were highlighted) occur mostly in stands with relatively low densities and larger diameters, which indicates old stands. When examining the two grand totals (diameter classes and density classes alone), there is only one basal area slightly larger than 40 m<sup>2</sup>/ha (41 m<sup>2</sup>/ha). Therefore, 40 m<sup>2</sup>/ha is defined to be the maximum basal area for pure aspen stands ( $BA_{AWmax}$ ).

Similar rationale was used to determine the maximum stand basal areas for the other two species and the mixtures of all species. The maximum basal area was 50 m<sup>2</sup>/ha for pure white spruce stands ( $BA_{SWmax}$ ) and 45 m<sup>2</sup>/ha for pure lodgepole pine stands ( $BA_{PLmax}$ ). When all species were combined in mixedwood stands, the maximum stand basal area was 55 m<sup>2</sup>/ha ( $BA_{ALLmax}$ ). It should be pointed out that the final selection was conditioned by the performances of these factors in MGM projections. The percentiles were used as a guide in defining these values due to lack of data in extreme stand conditions.

Maximum allowable stand volumes for dense density stands based on stand volumes from Alberta Normal Yield Tables (see Table 4.2) and the upper bound of stand volumes of the PSP data (see Table 4.3) were used to decide the constant  $m$  in equation (1). Different  $m$  values ranging from 50 to 200 were tried and a final value of 80 was chosen based on MGM simulations.

With the defined maximum stand basal areas and the constant  $m$ , the following constraining factors were derived:





$$F_{AW1} = \begin{cases} 1 - \frac{BA - BA_{AWmax}}{m} = 1 - \frac{BA - 40}{80} & (\text{if } BA > 40) \\ 1 & (\text{if } BA \leq 40) \end{cases} \quad (1a)$$

$$F_{SW1} = \begin{cases} 1 - \frac{BA - BA_{SWmax}}{m} = 1 - \frac{BA - 50}{80} & (\text{if } BA > 50) \\ 1 & (\text{if } BA \leq 50) \end{cases} \quad (1b)$$

$$F_{PL1} = \begin{cases} 1 - \frac{BA - BA_{PLmax}}{m} = 1 - \frac{BA - 45}{80} & (\text{if } BA > 45) \\ 1 & (\text{if } BA \leq 45) \end{cases} \quad (1c)$$

$$F_{ALL1} = \begin{cases} 1 - \frac{BA - BA_{ALLmax}}{m} = 1 - \frac{BA - 55}{80} & (\text{if } BA > 55) \\ 1 & (\text{if } BA \leq 55) \end{cases} \quad (1d)$$

where BA is projected stand basal area,  $F_{AW1}$ ,  $F_{SW1}$ , and  $F_{PL1}$ ,  $F_{ALL1}$  are the constraining factors for stands of pure aspen, pure white spruce, pure lodgepole pine, and mixedwood species, respectively.

When projecting a stand in MGM, once the projected stand basal area is larger than the defined maximum basal area, one of the factors (equations (1a) to (1d)) will be activated, depending on the species present in the stand. If the species composition of the leading species in a stand (the ratio of species basal area to stand total basal area) is less than 0.8, this stand is considered as a mixedwood stand and equation (1d) will be activated. Otherwise, the factor for pure species stand (the leading species) will be activated. Equation (2) will be subsequently used to reduce the survival rates of individual trees.

#### 4.4.2. Constraints for large trees

Table 4.6 shows the quadratic mean diameter percentiles for aspen, white spruce, and lodgepole pine. As discussed in Section 4.3.2, for each species, a value close to the 90<sup>th</sup> percentile of quadratic mean diameters was chosen to be the quadratic mean diameter threshold. Based on Table 4.6, the following threshold values were selected: 26 cm for aspen, 28 cm for white spruce, and 22 cm for lodgepole pine.

Following the guiding principles set in Section 4.3.2, the constant C in equation (3) was determined to be 100 after examining the behaviors of the constraining factors using different C values ranging from 50 to 200. With the defined quadratic mean diameter thresholds and the C value, equation (3) became:





$$Z = \frac{(QMD_{AW} - QMD_{AWlimit})^2}{100} = \frac{(QMD_{AW} - 22)^2}{100} \quad (\text{if } QMD_{AW} > 22) \quad (3a)$$

$$Z = \frac{(QMD_{SW} - QMD_{SWlimit})^2}{100} = \frac{(QMD_{SW} - 28)^2}{100} \quad (\text{if } QMD_{SW} > 28) \quad (3b)$$

$$Z = \frac{(QMD_{PL} - QMD_{PLlimit})^2}{100} = \frac{(QMD_{PL} - 26)^2}{100} \quad (\text{if } QMD_{PL} > 26) \quad (3c)$$

The constraining factor  $F_2$  can be subsequently determined by replacing  $Z$  in equation (4):

$$F_2 = \begin{cases} \frac{1 + Z * (QMD_{SP} / DBH)}{1 + Z} & (\text{if } QMD_{SP} > QMD_{SPlimit} \text{ and } DBH > QMD_{SP}) \\ 1 & \text{otherwise} \end{cases}$$

With a particular projected quadratic mean diameter of a stand,  $Z$  value is fixed. Therefore, the larger the diameter of an individual tree is compared to the projected quadratic mean diameter (i.e., smaller  $QMD_{SP}/DBH$ ), the smaller the factor  $F_2$  is, and therefore, the more reduction on the survival rate of this tree. However, the resulting survival probability of this tree is not necessarily smaller, depending on the magnitude of the predicted survival probability from the empirical survival function ( $P_s$  in equation (5)). On the other hand, for two trees with the same relative position in two different stands (same  $QMD_{SP}/DBH$  ratio), the one in the stand with larger projected quadratic mean diameter will receive more reduction on its survival rate compared to the other one in the stand with smaller projected quadratic mean diameter.

Table 4.7 presents a few example values of the constraining factor  $F_2$  for all three species. Stands with various quadratic mean diameters (up to 50 cm) larger than the defined limits are used to calculate  $Z$  values and various tree diameters (up to 55 cm) larger than stand quadratic mean diameters are used to calculate the factor  $F_2$ . Notice that  $F_2$  values are very close to 1 for stands with only slightly larger quadratic mean diameters compared to the defined limits. For example,  $F_2$  values are all above 0.97 for all sized trees in an aspen stand with a quadratic mean diameter of 24 cm, which is 2 cm above the quadratic mean diameter limit. Therefore, reductions on the survival rates of any sized trees are quite small. Only when stand quadratic mean diameters are big, large sized trees receive more reductions on their survival rates, which is expected ecologically.



The constraining factors for larger trees should not be used for intensively managed stands since quadratic mean diameters can easily reach the defined limits while these stands are quite young and healthy. The PSP data used for this study came from natural stands and therefore, the constraining factors for large trees are only applicable for natural stands.

#### 4.4.3. Constraints for old stand breakup

For aspen stands with the reference site index of 20 m, the height growth rate from the site index curve was about 6 cm at 130 years of breast height age. For lodgepole pine stands with the reference site index of 18 m, the height growth rate from the site index curve was about 5 cm at 140 years of breast height age. Therefore,  $HTINC_{ref}$  was 0.06 m for aspen and 0.05 m for lodgepole pine. Accordingly, the height growth threshold of the top height trees that initiate stand breakup for aspen stands with different site index values became:

$$HTINC_{AWlimit} = HTINC_{ref} * (SI/SI_{ref}) = 0.06 * (SI/20) \quad (6a)$$

The same height growth threshold for lodgepole pine was:

$$HTINC_{PLimit} = HTINC_{ref} * (SI/SI_{ref}) = 0.05 * (SI/18) \quad (6b)$$

For any aspen or lodgepole pine stand, if the average height growth rate of the top height trees is below the above defined height growth threshold, equation (8) will be activated to kill trees quickly and break up the stand.

The constant K in equation (8) determines the deterioration rate. After examining different values between 0 and 1, K was selected to be 0.9. For various survival probabilities at the beginning of stand breakup, the survival probabilities at different years after the initiation of stand breakup are given in Table 4.8 with K=0.9. If the survival probability of a tree is less than 0.05, it is generally considered dead. The results in Table 4.8 show that the lower the survival probability of a tree is at the beginning of stand breakup, the faster it dies out. It takes about 25 to 30 years for trees with survival probabilities over 0.8 at the beginning of stand breakup to die.

Therefore, stand breakup factors for aspen and lodgepole pine are:

$$F_{AW3} = \begin{cases} 0.9 & \text{(if } HTINC_{AW} < 0.06 * SI/20) \\ 1 & \text{(if } HTINC_{AW} \geq 0.06 * SI/20) \end{cases} \quad (7a)$$



$$F_{PLJ} = \begin{cases} 0.9 & (\text{if } HTINC_{PL} < 0.05 * SI/18) \\ 1 & (\text{if } HTINC_{PL} \geq 0.05 * SI/18) \end{cases} \quad (7b)$$

And equation (8) is subsequently used to reduce the survival rates of eligible trees, i.e., those in the same canopy layer as the top height trees.

All constraining factors developed in this study, together with the maximum size-density curve developed in Chapter 3, were incorporated into MGM to constrain its empirical mortality functions. Table 4.9 lists all the factors and the conditions to activate them. Figs. 4.2, 4.3, and 4.4 are the examples of the projected stand volume trajectories for aspen, lodgepole pine, and white spruce with various initial stand densities (600 stems/ha to 70,000 stems/ha) on three site classes (site indices 22 m, 18 m, and 14 m). It is clearly shown that the projected stand volumes do not go beyond a certain maximum even when initial stand densities are very high. In addition, short-lived aspen and lodgepole pine stands break up when approaching old ages. Aspen stands on good sites start the deterioration process earlier and disappeared completely at 160 years. This timing is delayed for some years for lower site classes (Fig. 4.2). Lodgepole pine stands have similar breakup patterns, except they stay a little bit longer (Fig. 4.3).

#### 4.5. Discussion and Conclusions

MGM simulations showed that projected stand volumes were too high for very dense stands. In addition, short-lived aspen and lodgepole pine stands still grew strongly at very old ages. Closer evaluation of the simulation results revealed that the empirical mortality functions in MGM caused these problems. The mortality rates were too low in both cases, which is not reasonable ecologically. The maximum size-density relationship developed in Chapter 3 was also based on the same data used for this study and therefore, same extrapolation problem existed in extreme conditions like very dense or very old stands.

Several theoretical factors were developed and incorporated into MGM to constrain its empirical mortality functions. Constraining factors based on maximum basal areas successfully reduced the survival rates of individual trees in dense stands and maintained stand volumes below a reasonable limit. For all three species, the survival rates of old trees were reduced using the constraining factors developed using the maximum and the projected quadratic mean diameters. Lack of stand breakup for short-lived aspen and lodgepole stands





was the result of high survival rates of trees in old stands. Constraining factors based on the average height growth of top height trees were able to break aspen and lodgepole pine stands around 150 to 200 years, depending on site qualities. Stands on good sites broke up early compared to stands on poor sites.

Lodgepole pine generally regenerates with high densities after fire. If the initial density of a stand is very high and the stand is on a very poor site, repression is likely to occur and tree height growth is reduced substantially. However, this density-caused height growth loss is not detectable in most cases, unless the initial stand density is extremely high. At lower densities (around 50,000 stems/ha), this growth loss is not identifiable (Mitchell and Goudie 1980, Goudie 1980). J.S. Thrower Assoc. (1993) suggested that this lower density was about 10,000 stems/ha at 30 to 40 year old stands. The density at the time of regeneration must have been a lot higher than 10,000 stems/ha if the self-thinning was operating.

Although lodgepole pine is generally considered less able to self-thin themselves at very high densities, no quantitative information is available as to what density repression occurs. Jim Goudie (Growth and Yield Biometrician, Ministry of Sustainable Resource Management in Victoria, personal communication) thinks that in dense lodgepole pine stands, mortality still occurs at a normal rate compared to height growth, only the repressed height growth causes it to be slower in terms of age. It seems that repression is less of a problem on good and medium sites. However, for very dense lodgepole pine stands on very poor sites, repression is likely to occur.

Therefore, the basal area constraining factor developed in this study should be applied with caution for lodgepole pine stands growing on poor sites. When repression occurs, trees are not dying much, as is usually the case for other species regulated by self-thinning. Therefore, although tree height and diameter growth rates are very small for individual trees, a large stand basal area might still occur due to the large number of trees in the stand. If the basal area constraint is activated, trees are forced to die out, which is not realistic ecologically. To be cautious, this factor was not applied for lodgepole pine stands growing on very poor sites.

The repression problem is very difficult to model and there is no quantitative information on the starting site quality below which repression would occur. For this study, the basal area



constraining factor was not applied to lodgepole pine stands with site indices below 12 m. As more information becomes available, this threshold value should be adjusted properly to reflect the ecological reality.

Aspen stands do not suffer repression from overstocking like lodgepole pine. When initial densities are high, stands will naturally thin themselves. Self-thinning occurs very early for stands with excessive initial densities. This is supported by many published research papers (Polland 1971, Bella and DeFranceschi 1980, Perala 1984, Bella 1986). After a major disturbance, aspen normally dominates the site quickly through root suckering with a large number of stems. In some extreme cases, the initial density can be as high as several million stems per hectare. Even at modest densities (around 20,000 stems/ha), there is still a very rapid reduction in density in the first 5 years. A reduction of 80% in stand density is not uncommon from year 1 to year 5 (Navratil and Bella 1988). For the Prairie Provinces, Navratil and Bella (1988) showed a 45% decrease in density in just 1 year, from year 2 to year 3.

White spruce normally does not regenerate into very dense stands. On the contrary, regeneration of white spruce has long been a problem in boreal mixedwood forests. A lot of work has to be done to improve white spruce regeneration (Johnstone 1976, Packee 1990, Lieffers and Beck 1994). However, we do occasionally get very dense white spruce stands regenerated (Grant Klappstein, forester, Alberta Sustainable Resource Development, Edmonton, personal communication). When this happens, the basal area constraint developed in this study will prevent unrealistically high volumes for these dense stands.

Unlike self-thinning mortality where smaller trees have higher mortality rates, larger trees have higher chance of dying out in old stands, especially in uneven-aged stands where larger trees are normally associated with old ages. Although the U-shaped mortality trend is captured by the diameter and diameter squared terms in the empirical survival functions developed in Chapter 2, the mortality rates for really large old trees are still not high enough due to inadequate data on these trees. The constraining factors based on the maximum quadratic mean diameter will further increase the mortality rates of those large old trees and enforce the U-shaped mortality trend.



The developed constraining factors based on the average height growth rate of top height trees will break up aspen and lodgepole pine stands at old ages. However, the timing of stand breakup, including the initiation and the speed of the breakup, is not yet well understood. In this study, the average height growth of the top height trees was used to initiate stand breakup and a constant value of 0.9 was universally applied to reduce the survival rates of all the old trees. This constraining factor should be re-evaluated as more ecological knowledge becomes available.

With all three types of constraining factors developed in this study and the maximum size-density curve developed in Chapter 3, the empirical mortality functions in MGM perform reasonably well when extrapolated. It should be pointed out that interpolations are always safer than extrapolations. Lack of data on extreme stand conditions makes MGM extrapolations unavoidable. This might be a common problem for most empirical growth models. Ideally, we need data on both typical as well as extreme stand conditions. However, this might not be easy to achieve practically. It may be more practical to design experiments to evaluate the growth of stands with extreme conditions. This will help us to define the theory as for how stands respond in extreme conditions. For data sets with limited data on extreme stand conditions such as those typically obtained with random or systematic sampling, the constraining factors developed in this study allow us to expand the application range of a growth model.

## References

- Alberta Energy and Natural Resources, 1985. Alberta phase 3 forest inventory: yield tables for unmanaged stands. ENR Report No 60a. Edmonton, Alberta, 227 p.
- Alberta Environmental Protection, 1991. Alberta vegetation inventory standards manual. Edmonton, Alberta, 53 p.
- Alberta Land and Forest Service, 1998. Land and forest service permanent sample plot field procedure manual., Edmonton, Alberta, 110 p.
- Barnes, B.V., Zak, D.R., Denton, S.R., and Spurr, S.H., 1998. Forest Ecology. 4<sup>th</sup> edition, John Wiley & Sons, Inc., 774 p.





- Beck, D.E., 1971. Height growth patterns and site index of white pine in the southern Appalachians. *For. Sci.*, 17, 252-260.
- Bella, I.E., 1986. Logging practices and subsequent development of aspen stand in east-central Saskatchewan. *For. Chron.*, 68, 432-437.
- Bella, I.E., and DeFranceschi, J.P., 1980. Biomass productivity of young aspen stands in western Canada. Info. Rep. NOR-X-219, Environ. Can., For. Serv., North For. Res. Cent., Edmonton, Alberta, 23 p.
- Burns, R.M., and Honkala, B.H., 1990. Silvics of North America. USDA For. Serv., Washington, D.C., Agriculture handbook 654, vol. 1, Conifers, 675 p.
- Cao, Q.V., 1994. A tree survival equation and diameter growth model for loblolly pine based on the self-thinning rule. *J. Appl. Ecol.*, 31, 693-698.
- Drew, T.H., and Flewelling, J.W., 1977. Some recent Japanese theories of yield density relationships and their application to Monterey pine plantations. *For. Sci.*, 23, 517-534.
- Fralish, J.S., 1972. Youth, maturity, and old age. *In*: Aspen: symposium proceedings. USDA For. Serv. Gen. Tech. Rep., NC-1, 154 p.
- Goudie, J.W., 1980. The effects of density on the growth and development of repressed lodgepole pine and suppressed inland Douglas-fir. Final contract report on EP 850.02, BC Ministry of Forests, Victoria.
- Hamilton, D.A. Jr., 1994. Uses and abuses of multipliers in the Stand Prognosis Model. USDA For Serv Gen Tech Rep INT-GRT-310, 9 p.
- Huang, S., 1992. Diameter and height growth models. Ph.D. thesis, University of Alberta, Canada, 202 p.
- Huang, S., Titus, S.J., and Klappstein, G., 1997a. A compatible height and site index model for young and mature aspen based on natural subregions. *For. Manage. Res. Note*, No. 8, Pub. No., T/355. Alberta Land and Forest Service, Edmonton, Alberta. 28 p.
- Huang, S., Titus, S.J., and Morgan, D., 1997b. Subregion-based compatible height and site index models for young and mature stands in Alberta: revisions and summaries (Part I). *For. Manage. Res. Note*, No. 9, Pub. No., T/389. Alberta Land and Forest Service, Edmonton, Alberta. 60 p.
- Hubbard, F.M., Bond, B.J., and Ryan, M.G., 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology*, 19, 165-172.
- Hynynen, J., 1993. Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. *Scand. J. For. Res.*, 8, 326-336.





- Johnstone, W.d., 1976. Ingress of lodgepole pine and white spruce regeneration following logging and scarification in west-central Alberta. Info. Rep. NOR-X-170, Northern For. Res. Centre., Edmonton, Alberta, 12 p.
- J.S. Thrower and Assoc., 1993. Paired-plot sampling for height growth repression and recovery in three older juvenile spacing projects in fire-origin lodgepole pine. Contract report to Silv. Branch, BC Ministry of Forests, Victoria.
- Köstner, B., Biron, P., Siegwolf, R., and Granier, A., 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor. Appl. Clim.*, 53, 105-113.
- Lieffers, V.J., Beck, J.A. Jr., 1994. A semi-natural approach to mixedwood management in the prairie provinces. *For. Chron.*, 70 (3), 260-264.
- Long, J.N., and Smith, F.W., 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *For. Ecol. Manage.*, 53, 53-64.
- Mitchell, K.J., and Goudie, J.W., 1980. Stagnant lodgepole pine. Progress report on EP 850.02, BC Ministry of Forests, Victoria. 31 p.
- Navratil, S., and Bella, I.E., 1988. Regeneration, development and density management in aspen stands. *In*: R.L. Gambles (eds). Management and utilization of Alberta's poplars. p 52-58. *Proc., Tenth Annua. Meet. Poplar Counc. Can., Fac. For. Univ. Toronto, Toronto, Ontario*, 154 p.
- Oliver, C.D., and Larson, B.C., 1996. Forest stand dynamics. Update edition, John Wiley & Sons, Inc., 520 p.
- Packee, E.C., 1990. White spruce regeneration on a blade-scarified Alaskan loess soil. *North J. Appl. For.*, 7 (3), 121-123.
- Peet, R.K., and Christensen, N.L., 1987. Competition and tree death. *Bioscience*, 37 (8), 586-595.
- Perala, D.A., 1984. How endemic injuries affect early growth of aspen suckers. *Can. J. For. Res.*, 14, 755-762.
- Peterson, E.B. and Peterson, N.M., 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. *For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1*, 252 p.
- Pollard, D.F.W., 1971. Mortality and annual changes in distribution of above-ground biomass in an aspen sucker stand. *Can. J. For. Res.*, 1, 262-266.
- Ryan, M.G., and Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. *BioScience*, 47 (4), 235-242.



- Ryan, M.G., Binkley, D., and Fownes, J.H., 1997. Age-related decline in forest productivity: patterns and process. *Advances in Ecol. Res.*, 27, 213-262.
- Smither, L.A., 1961. Lodgepole pine in Alberta. *Can. Dep. For. Bull. No. 127*, 153 p.
- Sterba, H., and Monserud, R.A., 1993. The maximum density concept applied to uneven-aged mixed-species stands. *For. Sci.*, 39 (3), 432-452.
- Waring, R.H., and Schlesinger, W.H., 1985. *Forest ecosystems: concepts and management*. Academic Press, New York, 340 p.
- Waring, R.H., 1987. Characteristics of trees predisposed to die. *BioScience*, 37(8), 569-574.
- Wykoff, W.R., Crookston, N.L., and Stage, A.R., 1982. User's guide to the stand prognosis model. *USDA For. Serv. Gen. Tech. Rep. INT-133*, 112 p.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.*, 40 (3), 513-527.
- Yoda, K., Kira, T., Ogawa, H., and Hozumi, K., 1963. Self thinning in overcrowded pure stand under cultivated and natural conditions. *Journal of Biology, Osaka City University*, 14, 107-129.
- Zeide, B., 1991. Self-thinning and stand density. *For. Sci.*, 37 (2), 517-523.



Table 4.1. Density percentiles for pure aspen, pure white spruce, pure lodgepole pine, and all species combined.

Percentiles	Aspen (stems/ha)	White spruce (stems/ha)	Lodgepole pine (stems/ha)	All (stems/ha)
100	7615	7209	18366	18366
99	6518	4619	10192	7673
95	4680	3432	5654	4900
90	3105	2371	4560	3531
75	1836	1657	3090	2130
50	1166	1181	1997	1310
25	845	855	1300	879
10	641	550	968	588
5	544	425	810	450
1	311	271	435	287

Table 4.2. Stand volumes (m<sup>3</sup>/ha) from Alberta Normal Yield Tables (Alberta Energy and Natural Resources 1985).

Species	Age	Site class		
		Good	Medium	Poor
Aspen	100	362.40	268.17	182.23
	150	431.20	327.66	228.68
Spruce	100	376.40	259.85	140.65
	150	495.33	381.47	242.19
Pine	100	414.68	317.85	220.00
	150	493.71	395.04	289.14

Note: site indices (at breast height age of 50 years) for good, medium and poor sites are 20 m, 16 m, and 12 m for aspen, 18 m, 13 m, and 8 m for white spruce, and 18 m, 14 m, and 10 m for lodgepole pine.





Table 4.3. Volume percentiles for aspen, white spruce, lodgepole pine, and all species combined based on Alberta PSP data.

Percentiles	Aspen	Spruce	Pine	All species
100	542.5	737.4	589.9	742.9
99	512.1	693.4	540.6	597.6
95	436.0	539.3	475.3	517.5
90	413.1	494.6	434.3	476.9
75	329.7	406.4	359.8	410.0

Note: all volumes are in m<sup>3</sup>/ha.

Table 4.4. Basal area percentiles for aspen, white spruce, lodgepole pine, and all species combined based on Alberta PSP data.

Percentiles	Aspen	Spruce	Pine	All
100	55.9	69.3	64.7	87.9
99	52.4	67.7	54.1	61.4
95	45.6	53.4	49.3	54.6
90	41.7	50.1	46.6	50.9
75	35.5	43.5	41.6	45.1
50	29.5	37.0	36.3	38.1

Note: all basal areas are in m<sup>2</sup>/ha.



Table 4.5. Summary of stand basal areas (m<sup>2</sup>/ha) by quadratic mean diameter and density classes for pure aspen.

Density class (stems/ha)	Quadratic mean diameter class (cm)									Total
	6-10	10-14	14-18	18-22	22-26	26-30	30-34	34-38	38-42	
<500					19	28	34	32	31	30
500-1500		15	25	34	38	<b>41</b>	<b>45</b>			34
1500-2500	9	28	37	<b>46</b>						34
2500-3500	23	30								29
3500-4500	26									26
4500-5500	30									30
5500-6500	32									32
6500-7500	26									26
7500-8500	26									26
Total	27	27	31	35	37	40	<b>41</b>	32	31	33

Note: Basal areas larger than 40 m<sup>2</sup>/ha are highlighted. An empty cell indicates that there is no data for that particular density-diameter combination.

Table 4.6. Quadratic mean diameter (cm) percentiles for aspen, white spruce, and lodgepole pine.

Percentiles	Aspen	White spruce	Lodgepole pine
100	40.90	43.07	33.36
99	36.38	38.93	29.23
95	28.14	32.92	23.92
90	26.33	28.27	22.09
75	22.62	24.64	18.87
50	18.87	21.30	15.00



Table 4.7. Values of factor  $F_2$  for different sized trees in stands with various quadratic mean diameters for all three species.

Species	QMD (cm)	Z	DBH (cm)							
			26	28	30	35	40	45	50	55
AW	24	0.04	0.997	0.995	0.992	0.988	0.985	0.982	0.980	0.978
	28	0.36			0.982	0.947	0.921	0.900	0.884	0.870
	34	1.44				0.983	0.911	0.856	0.811	0.775
	38	2.56					0.964	0.888	0.827	0.778
	40	3.24						0.915	0.847	0.792
	45	5.29							0.916	0.847
	50	7.84								0.919
PL	28	0.04			0.997	0.992	0.988	0.985	0.983	0.981
	30	0.16				0.980	0.966	0.954	0.945	0.937
	34	0.64				0.989	0.941	0.905	0.875	0.851
	38	1.44					0.970	0.908	0.858	0.818
	40	1.96						0.926	0.868	0.819
	45	3.61							0.922	0.858
	50	5.76								0.923
SW	30	0.16				0.980	0.966	0.954	0.945	0.937
	34	0.64				0.989	0.941	0.905	0.875	0.851
	38	1.44					0.970	0.908	0.858	0.818
	40	1.96						0.926	0.868	0.819
	45	3.61							0.922	0.858
	50	5.76								0.923

Note: AW, PL, and SW represent aspen, lodgepole pine, and white spruce, respectively.



Table 4.8. Survival probabilities at different years after the initiation of stand breakup using equations (7) and (8) with  $K = 0.9$  for trees with various survival probabilities ( $P_s$ ) at the beginning of stand breakup.

$P_s$	Years after the initiation of stand breakup					
	5	10	15	20	25	30
0.10	0.06	0.03	0.02	0.01	0.01	0.00
0.20	0.12	0.07	0.04	0.02	0.01	0.01
0.30	0.18	0.10	0.06	0.04	0.02	0.01
0.40	0.24	0.14	0.08	0.05	0.03	0.02
0.50	0.30	0.17	0.10	0.06	0.04	0.02
0.60	0.35	0.21	0.12	0.07	0.04	0.03
0.70	0.41	0.24	0.14	0.09	0.05	0.03
0.80	0.47	0.28	0.16	0.10	0.06	0.03
0.90	0.53	0.31	0.19	0.11	0.06	0.04
0.95	0.56	0.33	0.20	0.12	0.07	0.04
0.99	0.58	0.35	0.20	0.12	0.07	0.04





Table 4.9. All constraining factors developed in Chapter 3 and Chapter 4.

Factor type	Species	Factor
Maximum size-density curve	All species	$DEN_{max} = \left( \frac{1/QMD - 0.0078891809}{0.0003913343} \right)^{\frac{1}{0.609790581}}$ $F = \begin{cases} \left( \frac{DEN_{max} * DBH}{DEN * DBH_{qmax}} \right)^{0.2} & (\text{if } DEN > DEN_{max}) \\ 1 & (\text{if } DEN \leq DEN_{max}) \end{cases}$
Constraints for dense stands	AW	$F_{AW1} = \begin{cases} 1 - \frac{BA - BA_{AWmax}}{m} = 1 - \frac{BA - 40}{80} & (\text{if } BA > 40) \\ 1 & (\text{if } BA \leq 40) \end{cases}$
	SW	$F_{SW1} = \begin{cases} 1 - \frac{BA - BA_{SWmax}}{m} = 1 - \frac{BA - 50}{80} & (\text{if } BA > 50) \\ 1 & (\text{if } BA \leq 50) \end{cases}$
	PL	$F_{PL1} = \begin{cases} 1 - \frac{BA - BA_{PLmax}}{m} = 1 - \frac{BA - 45}{80} & (\text{if } BA > 45) \\ 1 & (\text{if } BA \leq 45) \end{cases}$
	ALL	$F_{ALL1} = \begin{cases} 1 - \frac{BA - BA_{ALLmax}}{m} = 1 - \frac{BA - 55}{80} & (\text{if } BA > 55) \\ 1 & (\text{if } BA \leq 55) \end{cases}$
Constraints for larger trees	AW	$Z = \frac{(QMD_{AW} - QMD_{AWlimit})^2}{100} = \frac{(QMD_{AW} - 22)^2}{100} \quad (\text{if } QMD_{AW} > 22)$
	SW	$Z = \frac{(QMD_{SW} - QMD_{SWlimit})^2}{100} = \frac{(QMD_{SW} - 28)^2}{100} \quad (\text{if } QMD_{SW} > 28)$
	PL	$Z = \frac{(QMD_{PL} - QMD_{PLlimit})^2}{100} = \frac{(QMD_{PL} - 22)^2}{100} \quad (\text{if } QMD_{PL} > 26)$
		$F_2 = \begin{cases} \frac{1 + Z * (QMD_{sp} / DBH)}{1 + Z} & (\text{if } QMD_{sp} > QMD_{splimit} \text{ and } DBH > QMD_{sp}) \\ 1 & \text{otherwise} \end{cases}$
Constraints for stand breakup	AW	$F_{AW3} = \begin{cases} 0.9 & (\text{if } HTINC_{AW} < 0.06 * SI/20) \\ 1 & (\text{if } HTINC_{AW} \geq 0.06 * SI/20) \end{cases}$
	PL	$F_{PL3} = \begin{cases} 0.9 & (\text{if } HTINC_{PL} < 0.05 * SI/18) \\ 1 & (\text{if } HTINC_{PL} \geq 0.05 * SI/18) \end{cases}$



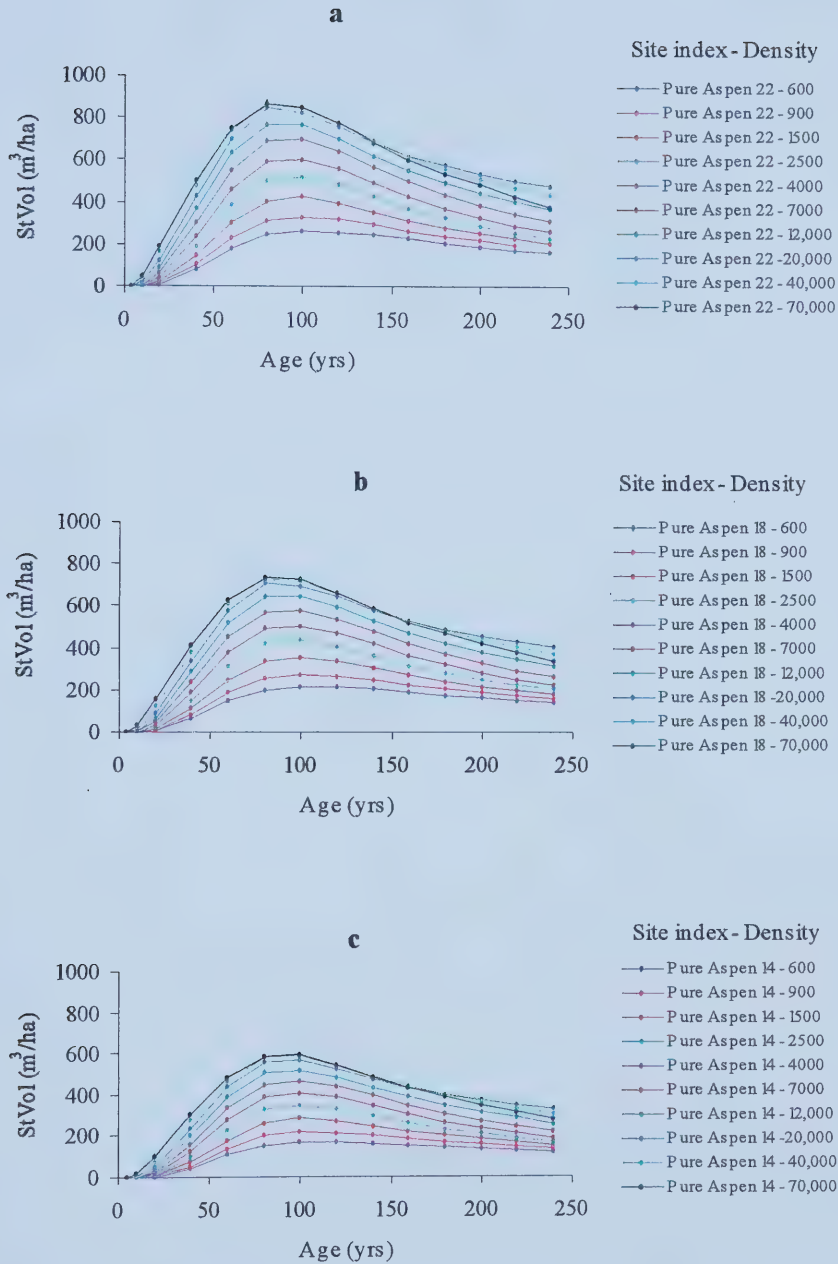


Figure 4.1. Volume trajectories of pure aspen stands of various initial densities on three sites without any constraining factor using the mortality functions developed in Chapter 2.



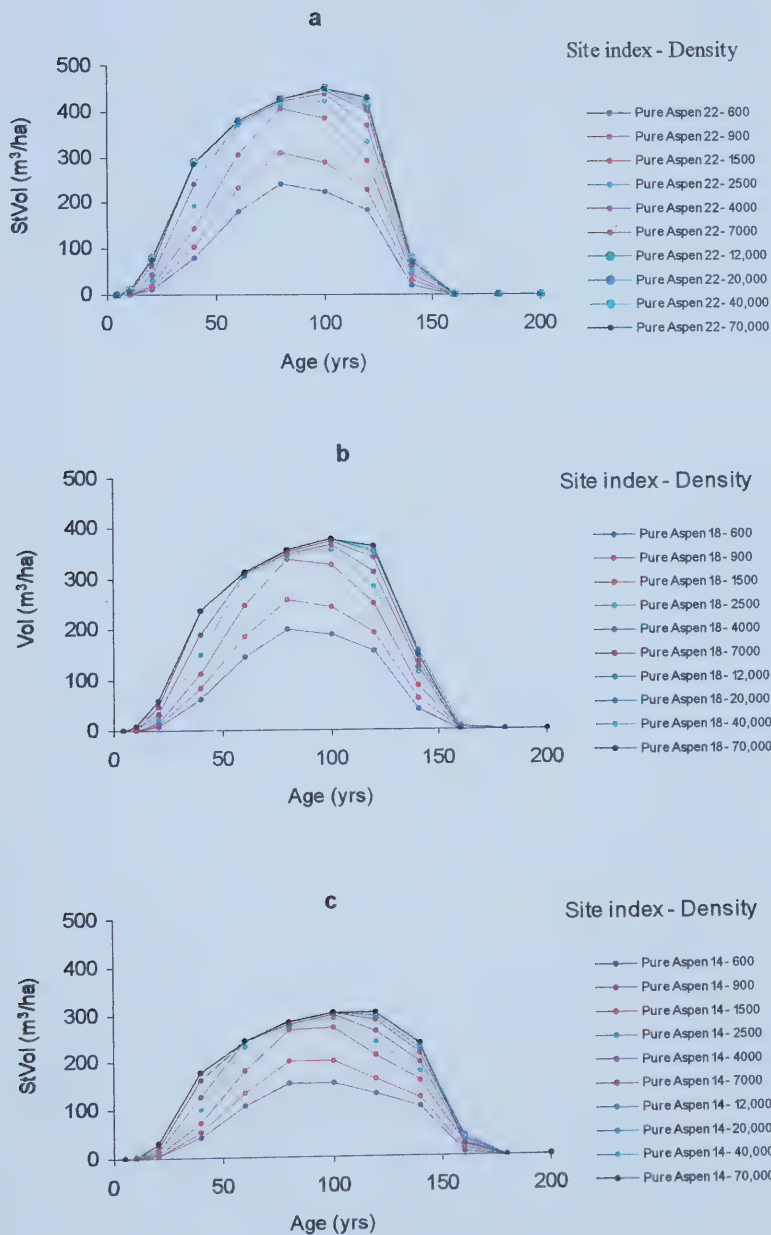


Figure 4.2. Volume trajectories of pure aspen stands of various initial densities on three sites with all constraining factors from this study and Chapter 3.



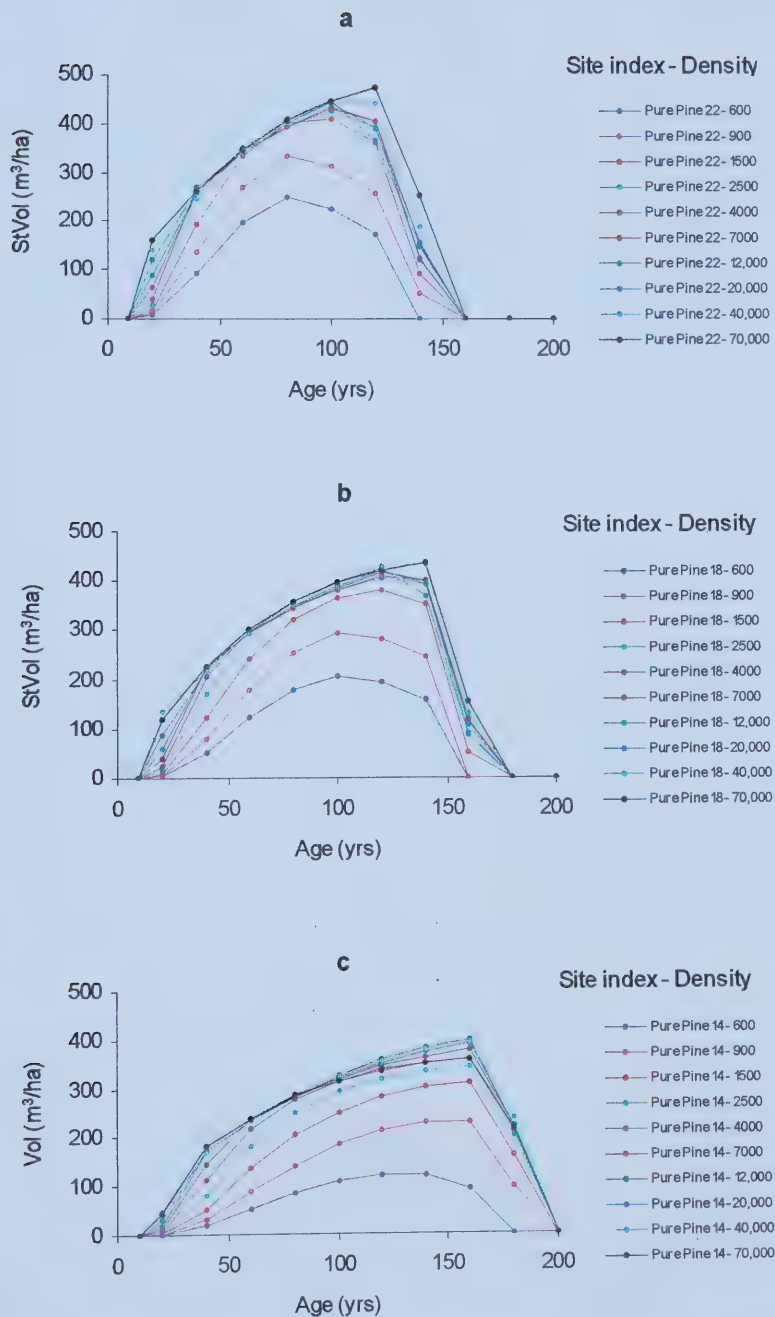


Figure 4.3. Volume trajectories of pure lodgepole pine stands of various initial densities on three sites with all constraining factors from this study and Chapter 3.





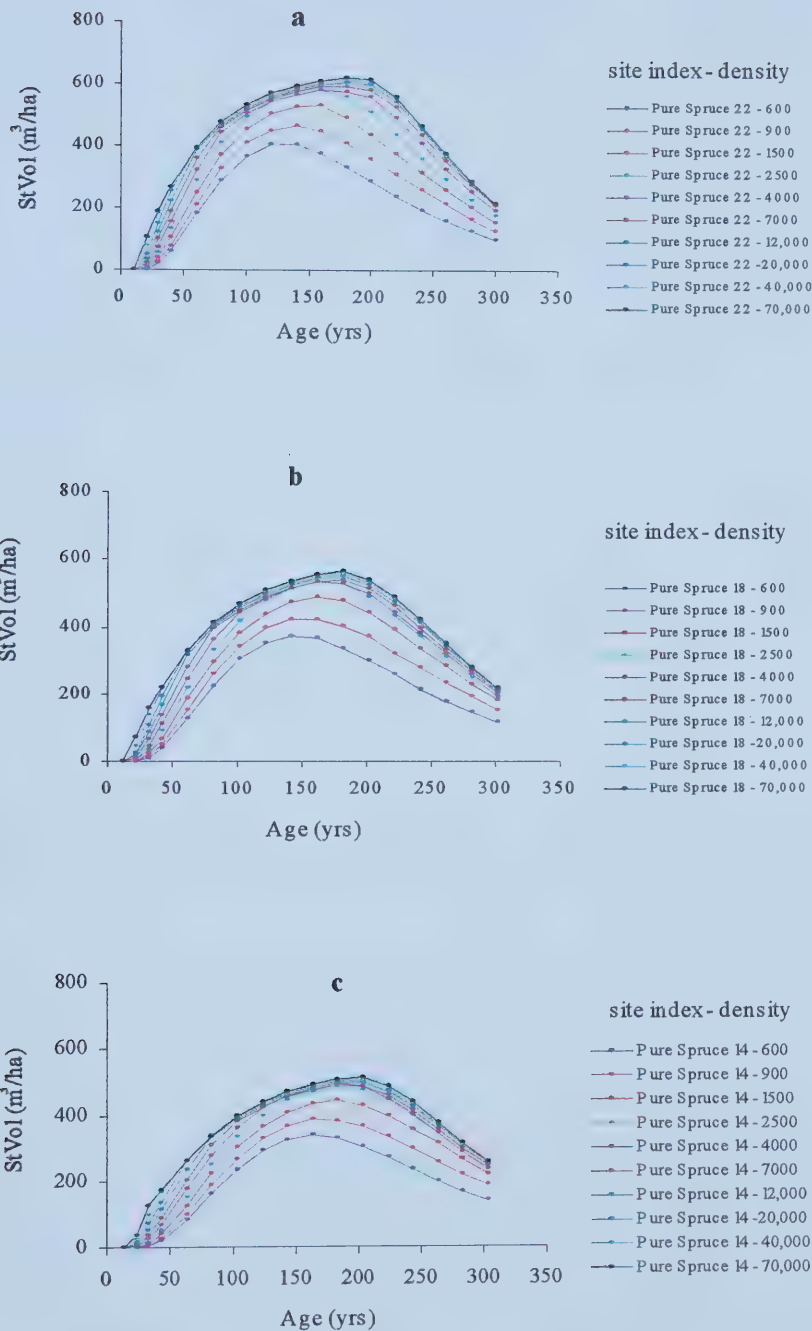


Figure 4.4. Volume trajectories of pure white spruce stands of various initial densities on three sites with all constraining factors from this study and Chapter 3.



## Chapter 5. Discussion and Conclusions

Due to the complexity in the process of tree mortality and the uncertainty in the timing of tree death, mortality remains one of the least understood components of growth and yield estimation. It is particularly so in multi-species boreal mixedwood forests. This thesis focused on mortality model development for three major boreal mixedwood species commonly occurring in Alberta: trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm).

Many factors can cause tree mortality and they vary among different stages of stand development. Although stand development is a continuous process, this process is often described by different phases. Peet, et al. (1987) defined 4 relatively distinct phases for the development of a stand after disturbance: the establishment phase, the thinning phase, the transition phase, and the steady-state phase.

At the establishment phase, tree mortality is very high due to stresses, pathogens and predators. Tree mortality rates are also highly variable due to the random nature of these factors. There is no or very little competition among trees at this phase.

As a stand continues to develop and reach canopy closure, the thinning phase starts and competition for light, water, and soil nutrients is intense. Smaller trees are at a competitive disadvantage compared to larger trees. They frequently fail the competition and die. The thinning process due to competition is commonly called self-thinning. Tree mortality at this stage is medium to high, depending on stand initial density. As pointed out by Peet, et al. (1987), if the establishment density of a stand is very low, the thinning phase might be bypassed altogether.

When competition-caused tree mortality converges to zero, a stand is in transition phase. Tree mortality rate at this phase is medium to low. Tree death is often density independent



(unrelated to competition) and is normally a consequence of pathogens, diseases, and some random events (Lloyd and Harms 1986). A stand eventually approaches the final stage (mature stage), or a steady stage (Peet, et al. 1987) after this transition phase. Again, tree mortality is caused by competition independent agents like pathogens, diseases, and some random events.

We can indeed add another phase to the development of forest stands, the old-age phase. At this phase, trees are normally large and less vigorous. Therefore, they are subject to wind damages and insect and disease attacks with increased mortality rates. This is demonstrated by the U-shaped mortality trend shown in Chapter 2.

At establishment stage, it is very difficult, if not impossible, to predict tree mortality by a mathematical model due to the highly variable mortality rates and unpredictable mortality agents. In this research, only trees in well-established stands (trees above 1.3 m in height) were modeled.

Out of the five growth stages, mortality at the self-thinning phase is relatively well defined because it is density dependent and size related. When self-thinning starts, competition for light, water and soil nutrients between individual trees becomes severe and trees die as a direct or indirect consequence of failing to compete successfully. At other stages, tree death is independent of density related competition and is caused by other mortality agents, some being random events.

The empirical survival functions developed in Chapter 2 did not differentiate self-thinning mortality from mortality caused by other agents. The dependent variable was coded as zero for all dead trees, no matter how they died. These empirical functions were able to accurately predict the survival probabilities of individual trees in typical stand conditions. Since the permanent sample plot data used in this study were not measured with equal time intervals, the length of measurement intervals appeared as an exponent in the equations, which resulted in generalized logistic functions. Instead of using automatic statistical procedures, potential predictor variables were selected based on their ecological importance to tree death. Variables diameter and diameter squared were included in all three survival functions to capture the U-shaped mortality trend, and diameter increment was used in all three functions to indicate tree



vigor. Since there were several competition related variables, only one or two of them were included based on their statistical contributions. The maximum likelihood method was employed to estimate the unknown parameters associated with predictor variables. Compared to the survival functions previously used in MGM, the new functions developed in this study performed better. This was supported by goodness-of-fit statistics and prediction statistics. After incorporating the new survival functions into MGM, simulations under a wide range of stand and site conditions further confirmed the better performances of the new functions.

In addition, species interactions were better modeled in the new survival functions, which was a major problem with the old survival functions. In typical mixedwood stands of aspen and white spruce, the unreasonable large impact of understory white spruce on the survival of overstory aspen was lessened by removing spruce species composition in the survival function of aspen. On the other hand, when overstory aspen density is low, it should have very little negative impact on the survival of understory white spruce, as shown by the new functions.

Although the developed logistic functions were empirical in nature, ecological and biological processes were incorporated in two ways. Firstly, the predictor variables were selected based on their ecological importance to tree mortality. A model developed from these variables was preferred, even at the expense of certain statistical properties. Secondly, potential functions were evaluated against ecological principles. Those that violated well-accepted ecological or biological theories were rejected even if they had good statistical fits. Evaluation results showed that the final logistic functions were ecologically reasonable. Therefore, the likelihood for the functions to perform well was increased both within and outside the data range used for model development.

A major concern about the old survival functions was that the projected stand volumes were too low for stands with very low initial densities. This was the case for all three species over a wide range of site qualities (Craig Farnden, forestry consultant, Prince George, personal communication). Using both the old and the new functions, four stands with lower initial densities of 600, 900, 1500, and 2500 stems/ha were projected for all three species. The new survival functions gave reasonable projected volumes for these low-density stands for all three species studied. Fig.5.1 was an example of projected stand volumes and densities for aspen stands on medium sites (site index 18 m). Figs. 5.1a and 5.1b were the projected stand





volumes and densities based on the new survival function, while Figs. 5.1c and 5.1d were the projected stand volumes and densities using the old survival function. With the old survival function, the maximum projected volume for the stand with 2500 stems/ha was less than 200 m<sup>3</sup>/ha, which was too low. When the new survival function was used, the maximum projected volume for the stand with 600 stems/ha was about 200 m<sup>3</sup>/ha. In addition, the density changes calculated from the new survival functions (Fig. 5.1b) are more reasonable compared to those calculated from the old functions (Fig. 5.1d). Using the old survival functions, there is almost no mortality for the first 30 years. Since all kinds of regular mortality are considered in both the new and the old functions, there should be some degree of mortality even if self-thinning related mortality is absent due to lower stand densities.

Besides the difference in mortality rates discussed above, other differences were also detected between the new and the old survival functions based on MGM simulations. For example, the new functions showed a much greater volume early in stand development with a substantial decline at older ages, while the projections using the older functions were almost asymptotically increasing, which is not realistic ecologically.

The empirical mortality functions developed in Chapter 2 behaved better than the old ones in typical stand conditions. However, they still gave unreasonable predictions when extrapolated. The maximum size-density relationship developed in Chapter 3 was based on the well-accepted self-thinning theory and was used as a theoretical constraint on the empirical survival functions. It was a simple relationship between quadratic mean diameter and stand density that defined an upper limit for stand development. Instead of fitting the relationship on log-log scale as is commonly done in applications of the self-thinning rule or Reineke's stand density index, original data were used. Site quality did not affect this relationship and it worked for mixedwood stands taken as a whole, not for each individual species in mixtures.

There are three model components in MGM: diameter growth functions, height growth functions, and mortality functions. Prediction errors from each component will be accumulated into yield predictions. In addition, due to the iterative nature of MGM, prediction errors will also be accumulated as model projection continues. The accumulated errors might be quite big when stands are projected for an extended period of time. With the developed



maximum size-density relationship, a stand will always be maintained on or below the upper limit and ensure reasonable stand level predictions.

The maximum size-density relationship can also be used as an effective way of ‘correcting’ the wrong MGM inputs given by inexperienced users. Accurate model inputs are critical for all growth models. This is not a problem when real data are used. The problem might occur for growth simulations where no real data are available. For a simulated stand as specified by a MGM user, the combination of quadratic mean diameter and stand density will be evaluated against the maximum size-density relationship. If the combination is above the upper boundary, the survival rates of individual trees will be reduced and bring the stand back onto or below the maximum size-density curve.

Chapter 4 presented the development of several theoretical factors used for constraining the empirical survival functions developed in Chapter 2. Without these factors, MGM simulations revealed bad model performances when extrapolated. Specifically, the problem is associated with very dense or very old stands. For all three species, projected stand volumes were too high for dense stands. In addition, for short-lived aspen and lodgepole pine, stands did not break up even when projected for a long period of time. Although predictor variables were selected based on their ecological importance, the developed survival functions are still empirical in nature. When extrapolated beyond the data range used for their development, it is not guaranteed that these functions will perform well. This is not surprising since an empirical function is the best fit of the available data and its predictive ability is always limited by the data. The developed constraining factors were based on ecological principles associated with stand dynamics and provided a level of comfort for applying MGM outside typical data ranges.

Although developed separately, all model components in MGM interact with each other and operate closely together. Diameter increment is an input variable for all three empirical survival functions and therefore, the diameter growth functions directly influence stand density changes predicted by the survival functions. Survival functions also affect the other two components due to the inclusion of some measure of stand density in the diameter growth functions and the height growth functions. All the constraining factors developed in this study



ensure reasonable stand level predictions and have the advantage of reducing the effects of possible poor interactions among the three model components in MGM.

On the other hand, lack of data has always been a problem faced by growth and yield modelers. Requirement for long-term measurement data covering the widest possible stand and site conditions makes it almost impossible to collect enough data to develop a 'perfect' growth model. The constraining factors developed in this study provide a level-of-comfort when applying a growth model like MGM outside the typical range of stand and site conditions as shown by Alberta PSP data.

All the objectives defined in Chapter 1 were achieved in this study. However, there is still plenty room for further research. For example, more research is needed to define the maximum stand basal areas for various stand types. In this study, the maximum basal areas were defined based on Alberta PSP data only and should be viewed as rough estimates. They should be adjusted as more reliable information becomes available. In addition, further research should be directed to study the timing of stand breakup for the short-lived aspen and lodgepole pine. Currently, accurate information on stand breakup is lacking and results from MGM long-term projections should not be considered as definite. As more information becomes available, the constraining factors responsible for aspen and lodgepole pine stand breakups should be reevaluated and modified if necessary.

## References

- Lloyd, F.T., and Harms, W.R., 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. *Annals of botany*, 57 (5), 681-688.
- Peet, R.K., and Christensen, N.L., 1987. Competition and tree death. *Bioscience*, 37 (8), 586-595.



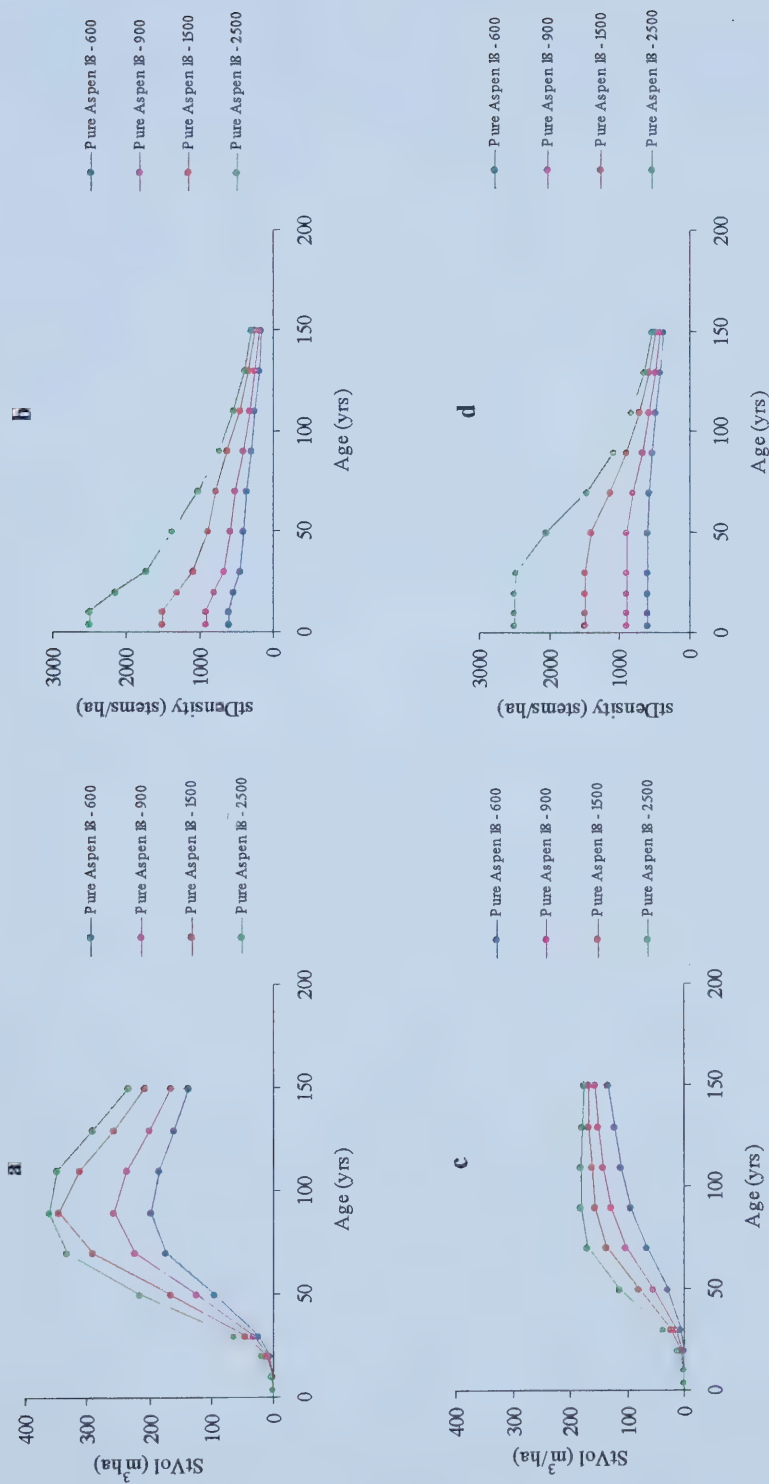


Figure 5.1. Comparisons of projected stand volumes and densities of aspen stands with site index 18 m using the new (a, b) and the old survival functions (c, d).





## Appendix I. The refitted survival function for aspen with white spruce species composition as a predictor variable

Previous literature suggests that understory trees should have very little impact on the survival of overstory trees (Kabzems et al. 1986, Kelty 1989). Therefore, aspen survival function developed in Chapter 2 does not include white spruce species composition as a predictor variable.

Dr. Vic Lieffers (professor, University of Alberta) commented during my thesis defense that in typical mixedwood stands of white spruce and aspen, white spruce trees in the understory might intercept a big portion of the precipitation and cause draught. Aspen is intolerant to draught and therefore, the survival rates of overstory aspen trees might be reduced with increasing understory white spruce trees. However, as pointed out by Dr. Uldis Silins (assistant professor, University of Alberta, personal communication), little quantitative information exists drawing a connection between differential interception rates among species and interactions with stand level water supply or productivity. Conceptually, it is assumed that as spruce develops in the understory that interception water losses may start to limit total stand water supply because spruce has higher leaf area. Presumably, this might affect crown water relations and stand productivity in many sites.

Due to the lack of quantitative information on the possible negative impact of understory spruce on the survival of overstory aspen, I decided to keep the original aspen survival function. However, for the benefit of future discussion, I refitted a new survival function for aspen with spruce species composition as an additional predictor variable, which is calculated as the ratio of spruce basal area to stand total basal area. The new survival function is given below:

$$P_S = \left[ 1 + \exp(-(\beta_0 + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DIN + \beta_4 * GGR * DBH^2 + \beta_5 * SC_{sw})) \right]^{-L}$$

where

$P_S$  = annual survival probability of an aspen tree

$DBH$  = individual tree diameter at breast height (cm)



- DIN = annual diameter increment (cm)
- GGR = basal area of larger trees (m<sup>2</sup>/ha)
- SC<sub>sw</sub> = white spruce species composition, defined as the ratio of spruce basal area to stand total basal area
- L = measurement interval length (yrs)
- $\beta_0 \sim \beta_5$  = estimated coefficients with  $\beta_0 = 2.311075766$ ,  $\beta_1 = 0.205438003$ ,  
 $\beta_2 = -0.002818697$ ,  $\beta_3 = 0.673323526$ ,  $\beta_4 = -0.000070453$ ,  
 $\beta_5 = -0.577397445$ .

Using this new survival function, understory spruce trees has quite big negative impact on the survival rates of overstory aspen trees, which may or may not be appropriate. This needs to be verified when new ecological information becomes available on the potential impact.

## References

- Kabzems, A., Kosowan, A.L., and Harris, W.C., 1986. Mixed section in an ecological perspective. 2<sup>nd</sup> edition. Forestry Division, Saskatchewan Parks and Renewable Resources, Saskatchewan. Tech. Bull. No. 8, 122 p.
- Kelty, M.J., 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage., 28, 237-257.



## Appendix II. SAS code for fitting the average and the maximum size-density relationships

**\*Fit the average size-density relationship using model (4);**

```
PROC NLIN DATA = FINAL BEST = 5 METHOD = MARQUARDT ITER = 200;
  MODEL QMD=1/(A+B*DENCLASS**C);
  PARMS A = 0.02 B = 0.0008 C = 0.54;
  DER.A=-1/(A+B*DENCLASS**C)**2;
  DER.B = -DENCLASS**C/(A+B*DENCLASS**C)**2;
  DER.C = -(A+B*DENCLASS**C)**(-2)*B*DENCLASS**C*LOG(DENCLASS);
  OUTPUT OUT = OUTPUT P = YHAT R = RESID SSE = SSE STUDENT = STU;
RUN;
```

**\* Fit the maximum size-density relationship using model (4);**

```
PROC NLIN DATA = FINAL BEST = 5 METHOD = MARQUARDT;
  TEMP=1/(a+b*DENCLASS**c);
  MODEL MAXQMD = TEMP;
  PARAMETERS A = 0.018 B = 0.00006 C = 0.82;
  _LOSS_ = TEMP - MAXQMD;
  IF (_LOSS_ < 0) THEN _LOSS_ = 20;
  OUTPUT OUT = ADJUST P = PREDICT;
RUN;
```

Note: QMD is quadratic mean diameter, DENCLASS is density class, and MAXQMD is the maximum quadratic mean diameter for each density class.

















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